PROCEEDINGS OF
THE LINNEAN SOCIETY OF LONDON
Session 1953–54

Vol. 166 Parts 1 and 2

PROCEEDINGS OF THE GENERAL MEETING HELD ON 8 October 1953

Lt.-Col. R. B. Seymour Sewell, C.I.E., F.R.S., President, in the Chair.

The Proceedings of the Anniversary Meeting held on Thursday, 28 May 1953, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—H.M. The Emperor of Japan, Dr. R. H. Ahrenfeldt, Dr. T. E. T. Bond, Miss Lucy M. Cranwell, Mr. Alan Fisk, Mr. S. S. Ghosh, Dr. Isabella Gordon, Dr. Olov Hedberg, Dr. Johannes Lid, Mr. R. Morse, Prof. R. E. G. Pichi-Sermolli, Mr. W. R. Price, Mr. B. W. Ribbons, Mr. F. R. G. Rountree, The Rev. H. Santapau, Dr. R. E. Schultes, Dr. E. E. Sherff, Lt.-Col. R. B. Seymour Sewell, C.I.E., F.R.S., Mr. N. Douglas Simpson, Dr. Edouard Thommen, Dr. Arvid H. Uggla, R.N.O., R.V.O., Mr. B. Verdcourt, St. George's Hospital Medical School, Messrs. Hutchinson & Co. Ltd., and Messrs. H. F. & G. Witherby, Ltd.

The following signed the Obligation in the Roll and Charter Book, and were admitted Fellows :—Dr. Thomas James Walsh, Dr. Effie Moira Rosser, Miss Joan Linnell Ivimy, Mr. Leslie Bilton, M.Sc., Mr. Stephen Benjamin Challen, B.Pharm., B.Sc., Mr. Walter William Pollard, B.Sc., Fg. Off. Gerald Haig Mickleburgh, and Mr. David Charles McClintock, M.A.

Certificates of recommendation for election to Fellowship were read for the first time in favour of the following :—Frederick Aldridge, Edavaleth Kakkat Janaki-Ammal, M.A., D.Sc., Henry Bennett Johnston, M.A., Miss Patricia Mann, B.Sc., A.L.S., Neil Boyd Watson McEacharn, Merfyn Richards, M.A., M.Sc., Ph.D., A.L.S., Horace Sinclair, Leslie Batten Currie Trotter, M.A., M.D., Frans Verdoorn, Ph.D., Peter James Wanstall, B.Sc., A.L.S., and Eric Clifford Wray, B.Sc.

The following communications were read and discussed :—

Dr. K. A. Kermack. An ancestral Crocodile from South Wales. (Discussed by Prof. D. M. S. Watson, F.R.S. and Dr. W. E. Swinton.)

Abstract—

During an extensive survey of fissures occurring in the Carboniferous Limestone of Glamorgan, carried out by Miss Robinson and myself in the Spring of 1952, a bone-bearing locality, probably of Upper Triassic age, was discovered at Pant-y-ffynon quarry, near Cowbridge. The bones are in an excellent state of preservation, and comprise five species of reptiles. The species best represented is a very primitive crocodile or crocodile ancestor. Of this animal there are several partially associated, and beautifully preserved skeletons known, along with a number of isolated bones. The beast was approximately two feet

in length and was very lightly built with long limbs and a very long tail. The skull is known by a fair amount of dissociated material but it has not yet been studied in detail. It is known, however, that there was a large antorbital vacuity. Some, at any rate, of the trunk vertebrae have both the rib articulations of the neural arch, this giving, in some specimens, the impression of two short transverse processes, one immediately behind the other. The pectoral girdle consists of a scapula, coracoid and large interclavicle. The coracoids were firmly articulated with the latter. The fore-limb is typically crocodilian, the carpus being reduced to four bones. These are the greatly elongated radiale and ulnare, the fused carpales 4 and 5 at the distal end of the latter, and a pisiform. There are two sacral vertebrae, both very crocodilian in appearance. The ilium and ischium resemble those of *Protosuchus*. The pubis is rather primitive, as it plays a part in the formation of the acetabulum, and is perforated by the obturator faramen. The median wall of the acetabulum is perforated by a small hole, as in all crocodiles. The hind limb is typically crocodilian in all repects, except that the fifth toe has two reduced phalanges, exactly as is figured by von Huene for *Erythrochampsa*. No body armour has so far been found. The importance of the above find is that it provides a ' missing link ' between the crocodiles and the thecodonts, the latter forming the basal archosaurian stock.

The animal has not so far been named, as the work of preparation is still proceeding and it is desired to nominate the best specimen as the type. This new find makes possible the identification of other previously known fossils as primitive crocodilians and suggest that the order arose in the Trias, as small, very agile land-living forms, and that the group did not take to its present aquatic habitat before the end of that geological period. This ecological niche had previously been filled by the unrelated Phytosauria.

Miss W. M. A. BROOKE, F.L.S. The vegetation of wet districts of the Bolivian Andes from 10,000 ft. to the snowline. (Discussed by Dr. J. G. Hawkes, Mr. A. H. G. Alston, Mr. E. J. H. Corner, Mrs. Vera Higgins and Mr. W. T. Stearn ; Miss Brooke replied.)

Abstract,—

Almost two years were spent collecting botanical specimens and seeds in remote districts of Bolivia. The country, which lies wholely in the tropics, varies in altitude from under 1,000 ft. to over 21,000 ft. Meteorological records give annual rainfalls of from 13 cm. to over 5 m. There are, therefore, great differences in vegetation and climate. A description, illustrated by drawings and slides, was given of the flora, and of the cold wet upper slopes of the Andes ranges to the East of the Altiplano and of Lake Titicaca. The flora includes numerous species of Gentian, tuberous Fuchsias, sessile Compositae, and a little known Lycopodium.

PROCEEDINGS OF THE GENERAL MEETING HELD ON 22 October 1953

Lt.-Col. R. B. SEYMOUR SEWELL, C.I.E., F.R.S. President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 8 October 1953, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Professor G. E. Hutchinson, Miss Stella Ross-Craig and Lt.-Col. R. B. Seymour Sewell, C.I.E., F.R.S., Pres.L.S.

The PRESIDENT reported the following deaths :—*Fellows:* David Miln, George Simpson, Thomas Paris, Eleanor Mary Reid, Cornelius van der Horst, Willoughby Gardner, Charles Blades Coverdale Storey, George Edward Nicholls, Amos Perry and Richard Higgins Burne, F.R.S. *Associate* honoris causa : Maude Jane Delap.

Certificates of recommendation for election to ordinary Associateship were read for the first time in favour of the following :—Anthony Frederick George DIXON, Robert Brian Ivimey-Cook, B.Sc., and Anthony Clive Jermy, and certificates of recommendation for election to Fellowship were read for the second time in favour of those candidates whose names appear in the Minutes of the Meeting held on 8 October 1953.

The following communication was read and discussed :—

Dr. J. HESLOP-HARRISON, F.R.S.E. The genus *Dactylorchis* in Britain a problem in variation. (Discussed by Mr. V. S. Summerhayes and Dr. W. B. Turrill; Dr. Heslop-Harrison replied.) **[Printed in full on p. 51.]**

PROCEEDINGS OF THE GENERAL MEETING HELD ON 19 November 1953

Lt.-Col. R. B. SEYMOUR SEWELL, C.I.E., F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 22 October 1953, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Dr. Isabella Gordon, Dr. L. Harrison Mathews, Dr. J. Ramsbottom, O.B.E., and Miss R. F. Shove.

The following signed the Obligation in the Roll and Charter Book, and were admitted Fellows :—Mr. Sydney Challenger and Lt.-Col. Donald Rhind, O.B.E.

The following candidates for Fellowship and Ordinary Associateship were balloted for and elected. FELLOWS :—Frederick Aldridge, Edavaleth Kakkat Janaki-Ammal, M.A., D.Sc., Henry Bennett Johnston, M.A., Miss Patricia Mann, B.Sc., A.L.S., Neil Boyd Watson McEacharn, Merfyn Richards, M.A., M.Sc., Ph.D., A.L.S., Horace Sinclair, Leslie Batten Currie Trotter, M.A., M.D., Frans Verdoorn, Ph.D., Peter James Wanstall, B.Sc., A.L.S. and Eric Clifford Wray, B.Sc. ORDINARY ASSOCIATES :—Anthony Frederick George Dixon, Robert Brian Ivimey-Cook, B.Sc., and Anthony Clive Jermy.

The following communications were read and discussed :—

Mr. N. WOODHEAD and Mr. R. D. TWEED. A consideration of the Freshwater Algae of Sierra Leone. (Discussed by Mr. R. Ross, Lt.-Col. D. Rhind, O.B.E. and Dr. George Taylor, Sec. L.S.; Mr. Woodhead replied.) **[Printed in full on p. 82.]**

Mr. G. Owen Evans. An Introduction to the External Morphology and Biology of the British Pseudoscorpiones (Arachnida). (Discussed by Dr. S. M. Manton, F.R.S., Dr. J. P. Harding, Dr. George Taylor, Sec. L.S. and Asst. Prof. H. R. Hewer.)

Abstract,—

An introductory account of the external morphology of the Pseudoscorpiones with reference to the classification and identification of the British species together with notes on methods of collecting, preparation for microscopical examination and biology. This lecture introduces a work on the British Pseudoscorpions in the *Synopses of the British Fauna,* **10**, 1954.

PRESIDENT'S RECEPTION,
3 December 1953

The President, Lt.-Col. R. B. Seymour Sewell, C.I.E., F.R.S., received the Guests in the Library.

Coloured and monochrome films, ' Underwater Cine-photography in the Ocean ', with a commentary by Mr. W. Deryck Chesterman, B.Sc., F.Inst.P. (Royal Naval Scientific Service), were shown in the Meeting Room.

Exhibits in the Library and Council Room.

London University Botanical Supply Unit. Decorative plants and young tropical trees. (Exhibited throughout the Library.)

The University of London Botanical Supply Unit was established about three years ago to supply the Colleges and Examinations Department of the University with botanical material. Much of this is grown in the grounds of the Unit at Englefield Green, Surrey, while collecting is also carried out in the surrounding countryside.

The Unit has now accumulated an extensive collection of plants. Among those exhibited are well known decorative plants and also a collection of young tropical trees, raised from seed from West Africa. These trees include specimens of Baobab (*Adansonia digitata*), Pawpaw (*Papaya carica*), Flamboyant or Flame of the Forest (*Poinciana pulcherrima*), Sand-box tree (*Hura crepitans*), *Thespesia lampas, Bauhinia monandra, Baphia pubescens, Cordia sebestena, Sterculia foetida,* and species of *Cassia, Albizzia* and *Peltophorum.*

Imperial College of Science and Technology.

(*a*) Apparatus for the Measurement of Micro-climates. [Shown by Mr. J. Walton Siddorn.]

The exhibit took the form of demonstrations of separate pieces of equipment for the assessment of temperature, relative humidity and solar radiation.

(i) *Temperature :* a demonstration of a simple thermocouple connected directly to a galvanometer.

(ii) *Relative humidity :* Jason's capacitance resistance hygrometer with with various elements.

(iii) *Solar radiation :* two original pieces of apparatus for the measurement of total solar radiation, diffuse and direct.

Plane type : a small chessboard of blackened and whitened copper squares connected in series by alternate wires of copper and constantan making a differential thermopile insensitive to changes in ambient temperature but registering on a galvanometer variations in incident thermal radiation. It registers only the vertical component of the radiation.

Spherical type : a modification of the chessboard pattern in which the elements are arranged over the surface of a sphere and enclosed in an evacuated glass flask. It is insensitive to change in direction of incident radiation and integrates such radiation from all directions. It can easily be made to record these variations and some typical records were shown.

(*b*) A Device for Recording the Activity of Ants. [Shown by Mr. J. Walton Siddorn.]

A colony of 500 worker ants (*Lasius flavus* L. in the Demonstration) is separated from its food (M/16 sucrose solution) by a glass tube through which the ants must pass on foraging journeys. This tube is of peculiar construction in its central portion and incorporates an insect valve designed to separate temporarily outgoing foragers from those returning to the ' nest '. During this separation the outgoing ants are counted by causing them to interrupt a beam of infra-red (and hence invisible) radiation incident upon a photoelectric cell. The pulses from the cell are amplified and they operate an electromagnetic counter which records the number of ants passing. In the original apparatus, consisting of two such units of which one is used as a control for the other, the figures on the counter are automatically photographed at half-hour intervals and the activity of the ants is thus registered in terms of ' foragers per half-hour '. This vector can be plotted against any variable ambient condition—e.g. temperature, light, type and strength of food—and the two quantities compared.

The apparatus is entirely automatic and needs no attention other than the daily (or weekly) changing of the photographic bromide paper on which the record is obtained. An electric ' monitor ' controls the stimulus under investigation and in a typical programme the sequence of events might be as follows :—

(i) Switch on.
(ii) Monitor starts camera after 3 hours (to allow for disturbance due to presence of observer at start.)
(iii) Monitor switches on stimulus (e.g. in temperature investigations, a heater in the cupboard containing the unit).
(iv) Monitor controls subsequent programme of stimulus (on-off, on-off, etc.) at predetermined intervals, this programme being recorded on the photograph beside the figures of the counters.
(v) Monitor switches off all electrical circuits in the correct order, finally turning itself off.
(vi) The photograph is removed and processed and the results plotted as described.

Mr. E. J. H. CORNER, F.L.S. Botanical Illustrations of Tropical Flowers.

BRITISH MUSEUM (NATURAL HISTORY). Blind Cave Fishes from Iraq, including living specimens. [Shown by Mr. N. B. Marshall.]

BRITISH MUSEUM (NATURAL HISTORY). Seaweeds of California. [Shown by Miss Linda M. Newton.]

The Californian coast supports one of the richest marine algal floras in the world, both in variety and quantity of weeds which flourish there. One factor contributing to the ideal growth conditions is the cold California Current, the continuation of the Aleutian Current of the North Pacific flowing southward between lat. 48° and 23°N where the Sub-arctic water converges with the Equatorial. The surface temperature of the water is further lowered in regions of spring upwelling, most conspicuous at 41° and 35°N, caused by the N–NW winds prevailing at this season. The spring water temperatures are thus lower than the winter temperatures and lower than those in regions south of 34°N, where the water has travelled a long distance as surface water. Although the upwelling is a very slow process and the water rises from moderate depths only, it is of the greatest importance to the productivity of the waters off the coast because the rising water brings nutrient salts into the upper zone where the light is sufficient for photosynthesis. It also happens that the inshore waters are considerably disturbed and so are consistently rich in oxygen to supply the needs of the vegetation of the rocky shores.

The plants exhibited ranged from *Macrocystis pyrifera* and *Gelidium cartilagineum*, commercially important for the production of alginates and agar respectively, the curious Sea Palm, *Postelsia palmaeformis*, which flourishes on the most exposed wave-lashed rocks, to the exquisite Red algae such as *Delesseria, Microcladia, Dasyopsis* and the corallines.

Royal Botanic Gardens, Kew. Photographs of *Kniphofia*. [Shown by Miss E. A. Bruce.]

The Zoological Society of London.

(*a*) Lizards of the family Gekkonidae. [Shown by Mr. J. W. Lester.]

(*b*) Land Crabs and Land Hermit Crabs. [Shown by Mr. L. C. Bushby.]

Mr. D. N. Paton, F.L.S., A.R.P.S. Coloured slides of some of the more striking of Pyrenean Flora.

During 1953, the author was able to make two short visits of a fortnight to the Pyrenees, one during April and the other during August. The object of these visits was to obtain coloured pictures of the flora. Although a visit during the most favourable month of June was impossible, yet over 100 coloured slides were collected. Some thirty of these were displayed.

Royal Botanic Gardens, Kew. The effect of flood water on *Wieglia rosea*. [Shown by Miss M. Whiting.]

Ministry of Agriculture and Fisheries (Veterinary Laboratory). Liverflukes and snails in Asia. [Shown by Dr. S. Brian Kendall.]

Throughout its range the liverfluke *Fasciola hepatica* is transmitted by snails which are very closely related both taxonomically and in their ecological requirements. The apparent multiplicity of vectors suggested by earlier authors is not confirmed when their systematic position is examined in the light of Hubendick's (1951) review of the *Lymnaeidae*. Similar considerations apply to *Fasciola gigantica* and its snail hosts.

In Asia the vectors of *Fasciola hepatica* and *F. gigantica* occur in the same geographical areas but in clearly differentiated habitats.

The demonstration compared the two species of *Fasciola* and their respective vectors (*Limnaea truncatula* and *L. auricularia rufescens*.) The different ecological requirements of the snails was illustrated.

Both these species of snail are maintained successfully at Weybridge. The emergence of cercariae following the experimental infection of snails was demonstrated. Ref. : Hubendick, B. (1951) Recent Lymnaeidae. *K. svenska Vetenska. Akad. Handl.* **3**(1).

THE PHARMACEUTICAL SOCIETY OF GREAT BRITAIN. Culinary Herbs and their Adulterants. [Shown by Dr. T. E. Wallis and Dr. J. M. Rowson.]

The exhibit showed a number of commercial samples of rubbed culinary herbs. The plants employed and the range of species were indicated.

Methods of identifying the rubbed herbs by macroscopical and microscopical characters were illustrated by diagrams, drawings and microscopical preparations.

The adulterants which had been found in certain culinary herbs were also shown with illustrations of their differential macroscopical and microscopical characters.

FRESHWATER BIOLOGICAL ASSOCIATION. The Entomostraca of moorland ponds near Windermere. [Shown by Mr. W. J. P. Smyly.]

Local distribution and seasonal periodicity are characteristic features of most species. In the open water only five species are abundant, *Diaptomus gracilis* (Copepoda) and *Daphnia longispina, Ceriodaphnia pulchella, Polyphemus pediculus* and *Diaphanosoma brachyurum* (Cladocera), and of these only the first two are also frequently found. In contrast some twenty common species have been taken in the rooted marginal vegetation. These latter species can be grouped broadly into three communities, those found associated with the floating leaves of *Potamogeton natans*, e.g. *Sida crystallina, Peracantha truncata* and *Alonella exigua* ; non-swimmers which crawl on or burrow in the surface film of bottom mud, e.g. *Ilyocryptus sordidus ;* lastly the true weed-dwellers which swim among, crawl on and attach themselves to the submerged stems of rooted plants. Members of this last group often show strong local distribution, e.g. a species may be abundant in *Nitella*, but scarce in *Carex* growing alongside.

Seasonal periodicity is shown by all species. Most species have their maxima in spring, summer and autumn but two Copepoda are most abundant in winter. Cladocera tend to be very abundant over rather short periods while Copepoda are less numerous over relatively long periods.

From collections over a year in two neighbouring ponds, one (Scale Tarn) in an open situation and with little rotting vegetation on the bottom, the other (Hodson Tarn) in a hollow between wooded slopes and with rotting Carex stems to a depth of a foot or more on the bottom of the only weed-bed, it was found that Scale Tarn supported a numerically greater open-water population than Hodson Tarn, and whereas in the weeds eleven abundant species in Scale were scarce in Hodson, only three species abundant in Hodson were scarce in Scale. What is known of the biology of these animals indicates that rotting vegetation in ponds may be regarded as a microhabitat where only relatively few species can live and thrive.

The problem of how freshwater Copepoda survive unfavourable conditions has aroused much speculation and interest among zoologists. Recently encysted copepodids (stage III) of *Cyclops bicolor* Sars were found in bottom mud of Scale Tarn and are believed to be the first record from Europe of a resting stage in Cyclopoida.

UNIVERSITY BOTANIC GARDEN, CAMBRIDGE. The History of the University Botanic Garden, Cambridge. [Shown by Mr. J. S. L. Gilmour.]

THE ZOOLOGICAL SOCIETY OF LONDON.

(*a*) Specimens illustrating the embryology of the Primates ; convergent evolution in fossil mammals ; and avian osteology. [Shown by Dr. W. C. Osman Hill.]

(*b*) Some interesting birds from the Society's Collection. [Shown by Mr. J. J. Yealland.]

British Museum (Natural History). The Espada fishery of Madeira, a series of photographs. [Shown by Mr. Denys W. Tucker.]

Off Madeira is one of the world's deepest fisheries, for the Black Scabbard-fish *Aphanopus carbo* Lowe, known locally as "*O Peixe Espada Preto*" or '*Espada*' for short. The catch of this bathypelagic species amounts to about 1,000,000 Kg. annually.

The fishery is practised mainly from Camara de Lobos by small open boats propelled by a sail and oars and carrying a crew of 4–6 men. Each vessel employs two long lines ('*Aparelhos das Espadas*'), each up to 1600–1800 metres in length with some 150–180 hooks on snoods towards its lower end and with a small stone weight at the extremity to make it hang steeply in the water, though without touching the bottom. Fishing is carried on at night and by the light of great torches. The boats lie about 4–5 miles offshore and drift some 8 hours with the lines down. Despite the great labour involved the lines are worked entirely by hand.

The pictures exhibited showed all stages of the fishery and marketing and included flashlight photographs of the actual fishing which are believed to be the first ever taken.

Royal Botanic Gardens, Kew. Researches on Knapweeds. [Shown by Dr. W. B. Turrill and Mr. E. M. Marsden-Jones.]

The Linnean Society of London. Rough draft by Linnaeus of a letter to Lady Monson (in Latin), with a translation by Dr. A. H. Uggla, F.M.L.S. [From the Linnaean Collections.]

PROCEEDINGS OF THE GENERAL MEETING HELD ON 7 January 1954

Lt.-Col. R. B. Seymour Sewell, C.I.E., F.R.S. President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 19 November 1953, having been circulated, were taken as read, and confirmed.

The President welcomed the presence at the Meeting of Professor Sven Horstadius, F.M.L.S., of Uppsala.

The following were thanked for gifts made to the Library since the last Meeting :—H.H. The Maharaja of Mysore, The Corporation of London, The Trustees of the British Museum, The Systematics Association, Dr. T. E. Wallis, Mr. S. J. Hughes, Mr. Richard Morse, Mr. I. H. Burkill and Dr. Francisco Mendonça.

The following signed the Obligation in the Roll and Charter Book, and were admitted Fellows :—Dr. Mary W. Parke, Miss Alice B. P. Stevens, B.Sc. and Mr. Horace Sinclair.

The PRESIDENT reported the death of Dr. George Parker Bidder, Fellow of the Society, and moved the following Resolution, which was passed in silence, all present standing in their places :—

> The Fellows of The Linnean Society of London have learned with the deepest sorrow of the death of Dr. George Parker Bidder, M.A., Sc.D., and desire to place on record their high appreciation of the great services he rendered to the Society in the thirty-five years of his Fellowship. Elected in 1919, he served on the Council from 1922 to 1926 and 1927 to 1933. He was appointed a Vice-President 1924–25 and again 1931–32 and was Zoological Secretary 1928 to 1931. During his Fellowship Dr. Bidder took the greatest interest in the work of the Society, and regularly attended its Meetings. Ever mindful of the great contributions Dr. Bidder made to Zoology, the Fellows desire to convey to Miss Bidder their deep sympathy on the loss of her distinguished father.

The following communication was read and discussed :—

Mr. ALAN DAVIDSON. Some Scandinavian Birds, illustrated with photographs, and a colour film of Lapland by Mr. Arthur Christiansen. (Discussed by Professor Sven Horstadius, F.M.L.S., Dr. J. Ramsbottom, O.B.E., Asst. Prof. H. R. Hewer and Lt.-Col. W. P. C. Tenison, D.S.O.; Mr. Davidson replied.)

Abstract,—

While resident in Denmark for some years after the war, I made a study of the birds of that country and undertook besides, expeditions to the Southern Swedish Highlands, the provinces of Nordland and Finnmark in Norway and Finnish Lapland north of the Arctic Circle. I was accompanied on some of these journeys by Mr. Arthur Christiansen, the well-known Danish bird photographer, whose work provided the illustrations to this lecture. Among the interesting species pictured and described were the Little Gull, Gull-billed Tern, Purple Sandpiper, Temminck's Stint, Pine Grosbeak, Long-tailed Skua, Bluethroat and Rustic Bunting.

PROCEEDINGS OF THE GENERAL MEETING HELD ON 21 January 1954

Lt.-Col. R. B. SEYMOUR SEWELL, C.I.E., F.R.S., President,
in the Chair.

The Proceedings of the General Meerting held on Thursday, 4 January 1954, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Professor Lily Newton, Professor A. J. E. Cave, Professor Dr. Alfred Ernst, Mr. W. T. Stearn, Dr. W. B. Turrill and Mr. F. C. Sawer.

The PRESIDENT reported the following deaths :—*Fellows:* Professor Henry Horatio Dixon, F.R.S. and Dr. Raphael Ernest Grail Armattoe. *Foreign Member :* Dr. Eugène Penard.

The PRESIDENT reminded Fellows, that nominations for Officers, New Members of Council, Foreign Members and Associates *honoris causa* should be forwarded to the General Secretary not later than 1 March 1954.

The following communication was read and discussed :—

Professor C. G. C. CHESTERS. Studies of the decomposition of seaweeds and seaweed products by micro-organisms. (Discussed by Miss L. Newton, Dr. Nellie Carter, Dr. J. Ramsbottom, O.B.E., and the President ; Professor Chesters replied.) **[Printed in full on p. 87.]**

The following papers were read in title :—

'Journey to the Gughé Highlands (Southern Ethiopia), 1948–1949 : Gastropoda, Slugs from the High Mountains.' By H. E. QUICK, B.Sc., F.R.C.S. (Communicated by Hugh Scott, Sc.D., F.R.S., F.L.S.)

'Journey to the Gughé Highlands (Southern Ethiopia), 1948–1949 : Coleoptera, Curculionidae, from the High Mountains.' By Sir GUY A. K. MARSHALL, F.R.S. (Communicated by Hugh Scott, Sc.D., F.R.S., F.L.S.)

The PRESIDENT read a letter from the Juniper Hall Field Centre, Dorking, inviting the interest of members of the Society in records being compiled at the Centre.

PROCEEDINGS OF THE GENERAL MEETING HELD ON 4 February 1954

Lt.-Col. R. B. SEYMOUR SEWELL, C.I.E., F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 21 January 1954, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Mr. M. R. Henderson, Sir Isaac Pitman & Sons, Ltd., Dr. Agnes Arber, F.R.S., and Dr. E. E. Sherff.

The following signed the Obligation in the Roll and Charter Book, and were admitted Fellows :—The Rt. Hon. The Viscount Chaplin and Mr. Peter James Wanstall.

The following communication was read and discussed :—

Dr. R. MELVILLE. Plant hunting across Australia 1952–1953 ; illustrated with projected Kodachrome transparencies. (Discussed by Dr. Hugh Scott, F.R.S., Dr. Max Pettersson, Dr. W. B. Turrill, Mr. E. J. H. Corner, Miss Nancy Burbidge, and Dr. J. Ramsbottom, O.B.E.; Dr. Melville replied.)

Abstract,—

The first introduction to the Australian flora of a traveller reaching Perth is in the nature reserve of Kings Park within the city limits. There, representatives of the laterite covered ridges and the sand plains that extend north to Geraldton may be seen. One hundred and fifty miles inland from Geraldton, 7-inch rainfall country is reached, which after heavy rains is clothed in a many coloured mantle of ephemerals. In taking the trans-continental route, a transect of increasing dryness is seen into the treeless Nullarbor. Victoria has a natural flower garden in the Grampians Mountains. A different mountain flora is seen above the tree line, as on Mt. Buller, and the lower slopes are clothed in Eucalypt forests, that contain some of the world's tallest trees. In the adjacent gullies tree ferns flourish. Contrasting with these associations are the salt marshes and mangrove swamps of Queensland. Everywhere fire, rabbits and man are making great changes in the flora and introduced weeds flourish exceedingly.

PROCEEDINGS OF THE GENERAL MEETING HELD ON 18 February 1954

Lt.-Col. R. B. SEYMOUR SEWELL, C.I.E., F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 4 February 1954, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Mr. I. H. Burkill, the Trustees of the British Museum, Mrs. W. E. Watson Baker, The Institute of Biology and Mr. R. W. J. Keay.

The PRESIDENT reported the following deaths :—Harry Britten, Associate *honoris causa* and Prabhat Chandra Sarbadhikari, Fellow.

The following signed the Obligation in the Roll and Charter Book, and were admitted Fellows :—Mr. Henry Bennett Johnston, M.A. and Dr. Leslie Batten Curie Trotter, M.A.

The following communication was read and discussed :—

Dr. JOHN SMART. Biotic zones on the West Coast of North America; illustrated with projected Kodachrome transparencies. (Discussed by Dr. W. Balfour Gourlay and Mr. N. Y. Sandwith ; Dr. Smart replied.)

Abstract,—

While on sabbatical leave from Cambridge, and as the fortunate recipient of a Smith-Mundt award from the U.S. Department of State and a Fullbright travel award, the lecturer spent the academic year 1952–53 with his headquarters in the Department of Entomology and Parasitology of the University of California, at Berkeley, California.

During 1953 opportunities arose to visit various localities as far apart as the Guatemalan border of Mexico in the south and the outlet of the Babine River from Lake Nilkitkwa in British Columbia in the north—a distance comprising 40° of latitude and approaching some 3500 flying-miles over-land.

It was in the U.S. section of this region that Grinnell and others developed and elaborated the idea of " Life Zones " originally put forward by Merriam. In the same area, and in California in particular, much work has been and is being carried out on speciation and evolution, matters closely related to ' Life ' or, as they are now more usually called, ' Biotic ' zones or areas. In the available time detailed studies of biotic zones were impossible but an effort was made to see examples of many of them.

California consists of a large plain, the floor of the Central Valley, surrounded by mountains except at one place where the Sacramento River drains out to the Pacific Ocean at San Francisco, and with a large desert area to the south-east. West, between the Central Valley and the ocean, are the Coastal Ranges ; east is the massive range of the Sierra Nevada ; northwards other mountain-join the Coastal Ranges with the Sierras while southwards the Tehachapi range does the same. The prevailing wind is from the west and there are, consequently, considerable differences in precipitation on the eastern and western sides of hills and mountains when these are of a size sufficient, along with other factors, to create a rain-shadow. Further east, beyond the Sierras and running more or less parallel to them, are further ranges of mountains such as the Inyo-White Mountain range.

The altitude of the Sierra Nevada (Sonora Pass, 9624 ft.) is such that one reaches Arctic-Alpine conditions above the timber-line on the peaks having passed from remnants of Lower Sonoran in the Central Valley, through Upper Sonoran in the Sierra foothills and the Transitional (forests) of the Sierras themselves. Thus all these and other biotic associations can be seen within easy distance of the Berkeley Campus.

Southern California is dryer than Central California. Large areas of desert (Lower Sonoran) occur and the dry forest (Upper Sonoran) ascends the mountains to a much greater altitude than it does in the Sierras. The Mojave Desert merges into the Colorado Desert and the other desert lands of Arizona. Northern California partakes of the heavily wooded nature (Transitional) of the western parts of the states of Oregon and Washington.

In the state of Chiapas, Mexico, the region visited was mainly within the Oak-Pine forest association of the central plateau of Chiapas ; tropical forest and thorn scrub associations were seen near the Guatemalan border. The desert regions (Sonoran) of North-West Mexico were seen, unfortunately, only from the air.

The biotic areas of British Columbia have recently been reviewed in outline by Munro and Cowan. Thanks to the assistance of Dominion and Provincial fisheries officers a very considerable part of the interior of the Province was visited and the following biotic areas seen :—Subalpine Forest, Cariboo Parklands, Columbia Forest, Coast Forest, Dry Forest and Osoyoos Dry Area.

PROCEEDINGS OF THE GENERAL MEETING HELD ON 4 March 1954

Lt.-Col. R. B. SEYMOUR SEWELL, C.I.E., F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on 18 February 1954, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—National Museum of Wales, British Society for the History of Science, Dr. Felix Widder, Society for the Promotion of Nature Reserves, Imperial College of Science, Royal University Library, Uppsala, Mr. O. B. Miller, I.S.O., and Mr. A. A. Bullock.

Certificates of recommendation for election to Fellowship were read for the first time in favour of :—Colin Booth, M.Sc., Kumud Chandra Bora, M.Sc., Ph.D., Miss Agnes Helen Stiell Brown, B.Sc., Ph.D., Humphrey Morrison Burkill, M.A., Henry Dodge, M.A., LL.B., Miss Clare Freda Lambert, B.Sc., Raymond Hedley Hudson, Harold Edgar Pidgeon, Basil Walston Ribbons, B.Sc., A.L.S., Henry Lindsay Gray Stroyan, M.A., and Denys William Tucker, B.Sc., A.L.S.

The following communication was read and discussed :—

Dr. HUGH SCOTT, F.R.S. Journey to the high Simien district (Northern Ethiopia) and the ancient cities of Axum and Gondar, 1952–3. (Discussed by the President, Mr. David Buxton, Mr. J. G. Esplen, Mr. J. B. Gillett, Mr. N. D. Riley, Mr. E. Milne-Redhead, Mrs. F. C. Stern and Mr. C. N. Hawkins ; Dr. Hugh Scott replied.)

Abstract,—

On journeys to central Ethiopia (1926–7) and to the Gughé Highlands (1948–9), collections were made on isolated massifs and extinct volcanic cones rising above the plateaux to heights from 10,000 to over 13,000 feet. The Simien district (over 500 miles north of Gughé) includes the greatest altitudes in Ethiopia, Ras Degien, the highest point, reaching 15,154 feet, while several others exceed 14,000 feet. Simien is isolated, the nearest massifs above 13,000 feet (Mt. Abuna Yosef, the Choké and other mountains) lying between 100 and 170 miles south-east and south.

The relationships of the Simien insects (never before systematically collected) with those of the central and southern mountains are of great interest. The plants were fairly well known from the work of Schimper and, recently, of Pichi-Sermolli, but valuable new material was obtained.

Simien was reached by a lorry journey of 270 miles southward from Asmara (Eritrea) to Debarec, the district centre, and thence by mule-caravan into the mountains. The stratoid volcanic rock forms extraordinary scenery ; immense precipitous escarpments with fantastic outlying towers and rock-castles ; on top, rolling grass and arable land, strewn with boulders, evidence of former extensive glaciation. In places too steep for cultivation, tree-heath forms a high, dense scrub, with bush-*Hypericum*, giant *Echinops*, *Kniphofia* and *Helichrysum*, while *Lobelia rhynchopetalum* grows over twenty feet high. A secondary scrub of *Juniperus procera* indicates that the cultivated land was formerly largely covered with coniferous forest, while groves of fine, lofty junipers are preserved round the churches. But no sign of the other conifer, *Podocarpus*, was seen. In the south of Simien wild olives are numerous in the valleys and on precipitous cliffs.

Some views were included of the castles and palaces built at Gondar during the Jesuit Mission (16th to 18th Centuries); also of the sculptured monoliths and the cathedral at Axum, centre of the culture derived from South Arabia several centuries B.C., from which rose the Christian Axumite realm in the 4th century A.D., and, eventually, late in the 13th century, the Amhara realm which continues to this day.

PROCEEDINGS OF THE GENERAL MEETING HELD ON 18 March 1954

Lt.-Col. R. B. SEYMOUR SEWELL, C.I.E., F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on 4 March 1954, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Mr. R. A. W. Lever, Dr. C. G. G. J. van Steenis, Mr. R. H. Jeffers, Mr. A. W. Rymer Roberts and The Royal Society.

The PRESIDENT reported the deaths of Arthur Anselm Pearson and James Pryde, Fellows of the Society.

Certificates of recommendation for election to Fellowship in favour of those candidates whose names were printed in the proceedings of the Meeting held on 4 March 1954 were read for the second time.

Certificates of recommendation for election to ordinary Associateship were read for the first time in favour of :—Peter Rutherford Gidlow Jackson, Ian Ronald Phelps, B.Sc., and Alwyne Cooper Wheeler.

The following communication was read :—

Dr. J. G. HAWKES. Taxonomic studies on the tuber-bearing Solanums—1 : *Solanum tuberosum* L. and the tetraploid species complex. **[Printed in full on p. 97.]**

PROCEEDINGS OF THE GENERAL MEETING HELD ON 22 April 1954

Lt.-Col. R. B. SEYMOUR SEWELL, C.I.E., F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on 18 March 1954, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Dr. Philippa C. Esdaile, Miss R. F. Shove, Mr. R. H. A. Plimmer, Dr. A. Tindell Hopwood and Dr. S. E. Chandler, O.B.E.

Mr. Frederick Aldridge signed the Obligation in the Roll and Charter Book and was admitted a Fellow.

The following were elected Auditors of the Treasurer's Accounts for 1953–54 under Chap. 10, Sect. 7 of the Bye-Laws :—

Representing the Council :	Mrs. F. L. BALFOUR-BROWNE, Dr. ALAN FISK.
Representing the Fellows :	Dr. M. A. P. MADGE, Mr. E. W. BAXTER.

Certificates of recommendation for election to membership were read for the first time in favour of the following :—*Foreign Members* :—Dr. Ernst Marcus of Sao Paulo, Brazil, and Dr. Arvid Hjalmar Uggla, R.N.O., R.V.O., of Uppsala, Sweden. *Associates* honoris causa :—Dr. John G. Dony, Reginald Henry Harris, A.M.A., George Burder Stratton, M.B.E., and Robert Orchard Williams, O.B.E. *Fellows* :—Arthur Rhys Beddows, M.Sc., Miss Margaret Collis, B.Sc., Ph.D., Mustafa Kamal, M.Sc., Kojo Obeng-Darko, Eric John Perkins, B.Sc., and Chandra Pal Singh, M.Sc.

The following candidates for Fellowship and Ordinary Associateship were balloted for and elected. FELLOWS :—Colin Booth, M.Sc., Kumud Chandra Bora, M.Sc., Ph.D., Miss Agnes Helen Stiell Brown, B.Sc., Ph.D., Humphrey Morrison Burkill, M.A., Henry Dodge, M.A., LL.B., Raymond Hedley Hudson, Miss Clare Freda Lambert, B.Sc., Harold Edgar Pidgeon, Basil Walston Ribbons, B.Sc., A.L.S., Henry Lindsay Gray Stroyan, M.A., Denys William Tucker, B.Sc., A.L.S. ORDINARY ASSOCIATES :—Peter Rutherford Gidlow Jackson, Ian Ronald Phelps, B.Sc., Alwyne Cooper Wheeler.

The following communication was read and discussed :—

Professor OVE ARBO HØEG. Spitsbergen, its present and past vegetation. (Illustrated by Monochrome and coloured slides.) (Discussed by Mr. E. J. H. Corner, Dr. J. Heslop-Harrison, Mr. F. Kingdon-ward, Dr. R. Melville and Dr. H. Hamshaw Thomas ; Professor Høeg replied.) **[Abstract on p. 144.]**

PROCEEDINGS OF THE GENERAL MEETING HELD ON 6 May 1954

Lt.-Col. R. B. SEYMOUR SEWELL, C.I.E., F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on 22 April 1954, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Sub-Dean of the Chapels Royal, Dr. W. B. Turrill, Mr E. Milne-Redhead, The Institute of Seaweed Research, Mr. F. W. Lindsay, Dr. L. Chalk, and Sir Norman Kinnear, C.B.

The following signed the Obligation in the Roll and Charter Book, and were admitted Fellows :—Mr. Colin Booth, M.Sc., Dr. Agnes Helen Stiell Brown, Mr. Raymond Hedley Hudson, Miss Clare Freda Lambert, B.Sc., Miss Patricia Mann, B.Sc., and Mr Neil Boyd Watson McEacharn.

Certificates of recommendation for election to Fellowship and Foreign Membership were read for the second time in favour of those named in the Proceedings of the General Meeting held on 22 April 1954.

The following communications were read and discussed,—

Mr. PETER SCOTT, C.B.E., D.S.C. A population study of the Pink-Footed Goose (illustrated by a film taken mainly in Iceland). (Discussed by Lt.-Col. W. P. C. Tenison, D.S.O. ; Mr. Scott replied.)

Mr. HUGH BOYD. Calculating methods used in the study.

Abstract of the two above papers combined,—

There is an urgent need for the development of methods of measuring wildfowl populations with sufficient accuracy for the early detection of significant increases or decreases in numbers. The Wildfowl Trust has undertaken a study of the Pink-Footed Goose (*Anser brachyrhynchus*) because it seems especially suitable for population measurement by the technique of ringing, as it is a species of limited geographical range and of comparatively small numbers. Ringing has been used for over 50 years to find out about the movements of wildfowl from reports of birds killed, and recoveries obtained in this way also give useful information on mortality but many biases limit the value of these data. If it is possible to catch sufficiently large numbers of geese at suitable intervals the proportion of recaptures of already marked birds will provide more accurate estimates of the population parameters.

The methods employed in capturing geese in such quantities took two forms, both of which will have been shown in the accompanying colour film. In Britain, in winter, rocket-propelled nets have been developed which can catch as many as 380 geese at one discharge.

The second method was employed in Iceland during the flightless period in July and early August, where the goslings are not yet able to fly and when the adults have moulted their flight feathers. Two expeditions were made to the centre of Iceland when on the first occasion (in 1951) a colony was found breeding on a large oasis near the Hofsjökull Ice-cap. This colony is believed to be the largest of the species in the world and in 1953 was estimated to have consisted of 8600 adults and 10,900 goslings. The flightless geese were captured by herding them on to the tops of hills and then driving them into portable nets. The method of herding, discovered in 1951 and developed in 1953, when a party of eight mounted on ponies was employed, must have resembled that used by the inhabitants of Central Iceland for several hundred years until the eighteenth century in catching geese for use as food. 1150 geese were caught in Iceland in 1951 and 9000 in 1953.

Recaptures and recoveries have shown that the British wintering population is largely independent of the much smaller population found in north Germany and Denmark. The British population appears to breed in Iceland and Greenland. The only other known breeding grounds are in Spitsbergen. Geese ringed there in 1952 by an expedition from Sherborne School have been recovered in Denmark and Germany but not in Britain.

The size of the British wintering population has been estimated from the proportion of recapture in successive years, using methods developed by Bailey. In 1952 and 1953 it was of the order of 36,000–41,000 in early autumn. Estimates of mortality from recaptures and recoveries both indicate an annual loss of the order of about 26 per cent of adults. The replacement of losses of this magnitude appears to be well within the reproductive capacity of the species.

Dr. W. J. L. Sladen, M.B.E. A preliminary report on the flora of the area illustrated with coloured slides.

The following papers were read in title :—

A new Ascidicolous Copepod. *Lichomoglas didemni*. By R. V. Gotto. (Communicated by Eric Ashby, D.Sc.)

The Polychaeta of South Africa, Part 3. Sedentary species from Cape Shores and Estuaries. By J. H. Day.

The Origin of the early European Potato. By R. Salaman.

Observations on the luminescence of bathypelagic Crustacea Decapoda of the Bermuda area. By R. Dennell.

The Wild Fodder Sorghums of the Section Eu-Sorghum. By J. D. Snowden.

Notes on the Algae Compsopogon. By F. R. Jones.

The Marine Algae of New Zealand, Part 1. By V. J. Chapman.

Two new Wingless species of Diptera, Sphaeroceridae (Borboridae), from Ethiopia. By O. W. Richards. (Communicated by Hugh Scott, Sc.D., F.R.S.)

PROCEEDINGS OF THE ANNIVERSARY MEETING HELD ON 24 May 1954

Lt.-Col. R. B. Seymour Sewell, C.I.E., F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 6 May 1954, having been circulated, were taken as read, and confirmed.

The President announced that a Loyal Message reading as follows had been sent to Her Majesty The Queen, Patron of the Society, upon her safe return from the Commonwealth tour.

> The President, Council and Fellows of The Linnean Society of London Assembled at their Anniversary Meeting at Burlington House wish to send to your Majesty the Patron of the Society in humble duty their Loyal Greetings and express their Happiness and Pleasure at the safe return of Your Majesty and H.R.H. The Duke of Edinburgh from the most successful and arduous journey to the countries of the Commonwealth.

The following were thanked for gifts made to the Library since the last Meeting :—Dr. Ulrik Røen, Mr. A. E. Blake, K.L.B., The Swedish Chamber of Commerce, Imperial Chemical Industries Limited, The Institute of Biology, Mr. B. Verdcourt, Ministry of Agriculture, Khartoum, and Mr. R. W. J. Keay.

The following signed the Obligation in the Roll and Charter Book, and were admitted Fellows:—Mr. Denys William Tucker, B.Sc., Mr. Eric Clifford Wray, B.Sc., Mr. Harold Edgar Pidgeon, Dr. Jacob Seide, Dr. Percy James Greenway, O.B.E., and Mr. John Bevington Gillett.

The PRESIDENT reported the death of Professor Felix Eugen Fritsch, F.R.S., Fellow of the Society, and moved the following Resolution, which was passed in silence, all present standing in their places :—

The Fellows of The Linnean Society of London, having heard with the very deepest sorrow of the death of Professor Felix Eugen FRITSCH, F.R.S., desire to place on record their high appreciation of the service rendered to the Society during his fifty-one years of Fellowship. Elected in 1903 he served on the Council from 1922–26 and 1949–53. He was appointed Vice-President 1925–26 and 1952–53, and held the Office of President from 1949–52. During his long Fellowship of the Society he showed the greatest interest in all its activities, being frequently present at its Meetings and a regular reader in the Library.

This year the Council had nominated Professor Fritsch for the award of the Linnean Gold Medal in appreciation of his great contributions to the study of Botany, and it is an added sorrow that the Award of the Medal to-day, on our Anniversary Meeting, must be posthumous.

Deploring the great loss of so distinguished a Fellow and really true friend of the Linnean Society, the Fellows desire to express to Mrs. Fritsch and her family their deepest sympathy in their bereavement.

Candidates for membership were balloted for and elected :—

Fellows.—Arthur Rhys Beddows, M.Sc., Miss Margaret Collis, B.Sc., Ph.D., Mustafa Kamal, M.Sc., Kojo Obeng-Darko, Eric John Perkins, B.Sc., and Chandra Pal Singh, M.Sc.

Foreign Members.—Dr. Ernst Marcus and Dr. Arvid Hjalmar Uggla, R.N.O., R.V.O.

Associate honoris causa.—Dr. John G. Dony, Reginald Henry Harris, A.M.A., George Burder Stratton, M.B.E., and Robert Orchard Williams, O.B.E.

The Bye-Laws regulating the Election of Council and Officers having been read by the General Secretary, the President declared the Ballot for new Members of Council to be open, and voting began. The President thereafter appointed Dr. J. G. Cockburn, Mr. R. H. Jeffers and Dr. H. S. Holden, as Scrutineers of the Ballot.

The Ballot was closed at the due time, and the result declared to the Meeting.—NEW MEMBERS OF COUNCIL.—Mr. E. J. H. Corner, Dr. M. A. P. Madge, Dr. T. C. S. Morrison-Scott, D.S.C., Dr. C. F. A. Pantin, F.R.S., and Miss E. M. Wakefield, O.B.E.

(The retiring Councillors were Mrs. F. L. Balfour-Browne, Dr. Alan Fisk, Dr. B. M. Hobby, Prof. F. W. Jane and Mr. Patrick M. Synge.)

The PRESIDENT declared the Ballot of Officers to be open and voting began. The ballot was closed at the due time, and the result declared to the Meeting.

—OFFICERS.—*President* : Lt.-Col. R. B. SEYMOUR SEWELL, C.I.E., F.R.S. ; *Treasurer* : Colonel F. C. STERN, O.B.E., M.C. ; *Zoological Secretary* : Mr. H. R. HEWER, M.Sc. ; *Botanical Secretary* : Dr. George TAYLOR.

In handing the Trail Award and Medal to Professor Irene Manton, the PRESIDENT spoke as follows :—

PROFESSOR IRENE MANTON has contributed much to knowledge of the structure of protoplasm. Her earlier work was largely concerned with the study of the spiral structure of chromosomes, using refined staining techniques. This led her to consider the whole question of fibrous structure in protoplasm. The electron microscope was the obvious tool to employ but, since chromosomes are not readily isolated from the cell, she turned her attention to flagella which, like chromosomes, have a fibrous structure but, unlike chromosomes, can be obtained free from cellular contamination. She and her co-workers have made an extensive and elegant contribution to knowledge of the fine structure of flagella in flagellates, algae and primitive fungi. This has greatly increased knowledge of the detailed structure of this specialized kind of protoplasm and has revealed the remarkable fact that the flagellum is an eleven-strand structure in all the plant groups so far studied.

Aside from her work on protoplasmic structure, Professor Manton has made brilliant contributions to the cyto-taxonomy of the British Pteridophyta.

In making the posthumous Award of the Linnean Gold Medal to Professor F. E. Fritsch, F.R.S., the PRESIDENT spoke as follows :—

In awarding the Gold Medal to PROFESSOR EUGEN FRITSCH we had recognized appropriately both his position as a leader in the study of the Taxonomy of the Freshwater Algae and a lifetime devoted to contributions to the advancement of our knowledge in this field. It is, indeed, now more than half a century since Fritsch published his first paper dealing with algal periodicity based on work carried out whilst he was attached to the Jodrell Laboratory in the Royal Botanic Gardens at Kew. There he investigated the seasonal changes in the phytoplankton of the river Thames which led to his subsequent and more intensive observations, extending through several seasons, of the algal populations of aquatic habitats in Somerset, in Hertfordshire and elsewhere, studies which clearly demonstrated the periodic character of the changes and inaugurated the enquiry into their causes.

Soon it became obvious that the mantle of Professor G. S. West had fallen upon Fritsch, for there followed accounts of the material collected by the Discovery Expedition from the Antarctic, on the one hand, on the other of collections made by himself from Ceylon. Later appeared accounts of tropical algae, extensive studies of the algae from South Africa, from Natal and from Griqualand. All these together, with continuing investigations of the fresh water and terrestrial algal flora of Britain itself, established and enhanced Fritsch's reputation as an authority on the systematics of the group with a breadth of experience that has seldom been equalled.

A lasting monument to Professor Fritsch's labours for algology are the two volumes on *The Structure and Reproduction of the Algae* which appeared in 1935 and 1945 respectively together with the revision of West's *Treatise of British Freshwater Algae* that was published in 1927. To these more special contributions to the advancement of algology must be added the more general but no less noteworthy assistance that was rendered by his initiative in the establishment of the British Freshwater Biological Station and to him in no small degree is due its subsequent success.

Not least the Linnean Society pays tribute to one who, besides being eminent for his contributions to cryptogamic studies, rendered great services during his term of office as President.

GENERAL SECRETARY'S REPORT

List of the Society.

Since the last Anniversary Meeting the Society has lost 34 members. The detailed statement is as follows :—

19 *Fellows by death :*

Raphael Ernest Grail Armattoe.
George Parker Bidder.
Edward Augustus Bowles.
Richard Higgins Burne.
Henry Horatius Dixon.
Felix Eugen Fritsch.
Willoughby Gardner.
Arthur John Ivens.
David Miln.
George Edward Nicholls.
Thomas Paris.
Arthur Anselm Pearson.
Amos Perry.
James Pryde.
Eleanor Mary Reid.
Prabhat Chandra Sarbadhikari.
George Simpson.
Charles Blades Storey.
Cornelius Jan van der Horst.

1 *Foreign Member by death :*

Eugène Penard.

2 *Associates* honoris causa *by death :*

Harry Britten.
Maude Jane Delap.

11 *Fellows by Withdrawal :*

John Evan Adlard.
Michael Robin Alexander Chance.
Earle Leslie Davison.
Harold Gorvett.
Kenneth John Hodges.
Sylvia Mavis Main.
Alec Lindsay Poole.
Baini Prashad.
James Stirling.
Kenneth Swinburne.
Winifred Margaret Warden.

1 *Fellow removed for non-payment of Annual Contributions :*

Syama Prasad Raychaudhuri.

During the Session, 28 Fellows, 2 Foreign Members, 4 Associates *honoris causa* and 6 Ordinary Associates have been elected. The number of Fellows on the list is 819 with a further 2 Fellows elected but not yet qualified. Foreign Members 50, Associates *honoris causa* 25 and Ordinary Associates 32 (5 Ordinary Associates have been elected Fellows during the Session).

The Library.

Between 1 May 1953 and 30 April 1954, 64 books have been purchased, 37 books, 120 parts of periodical publications and 61 reprints have been presented.

During the same period the number of volumes bound was 249.

The number of volumes borrowed was 1074—by Fellows and Associates 730 and 344 by the National Central Library.

611 signatures were recorded in the Library Visitors' Book.

THE PRESIDENT'S REVIEW

During the past Session, the 166th in our history, the usual number of General Meetings has been held and the standard of Communications to the Society has been well maintained. There has been a steady increase in the number of Communications that have been illustrated by colour-films and slides ; and among those worthy of special mention were Dr. Melville's account of " Plant Hunting across Australia ", Dr. Smart's account of " Biotic Zones on the West Coast of North America ", Prof. Høeg's account of " Spitsbergen, its present and past Vegetation " and the account given by Mr. Peter Scott and his Colleagues of their investigations in a " Population Study of the Pink-footed Goose ".

The number of Fellows of the Society is now 819 ; 28 new Fellows were elected during the past year but we have lost 30 by death or resignation. Among our losses by death special mention must be made of :—

Richard Higgins Burne, F.R.S., who joined the Society in 1912 and who served on the Council for several terms of office and was a Vice-President in 1925–26 and again in 1938–39.

George Parker Bidder, who joined in 1919, was a Member of Council for three terms of office and served as Zoological Secretary from 1928 to 1931 and was Vice-President in 1924–25 and again in 1931–32.

Professor *Henry Horatius Dixon*, F.R.S., who joined us in 1925.

Lord Aberconway, who was elected in 1927, served on the Council from 1933 to 1935 and was Vice-President in 1933–34 ; and

Professor *Felix Eugen Fritsch*, F.R.S., our President from 1949 to 1952, whose death I have already announced.

At the Memorial Service to Professor Dixon, held in Dublin, the Society was represented by Mr. G. W. Dawson, of Trinity College, Dublin ; and at the Memorial Service to Dr. Bidder, held in the Chapel of his old College, Trinity College, Cambridge, I was the Society's Representative.

On 2 June 1953, our Patron, Her Majesty Queen Elizabeth II, was crowned in Westminster Abbey and on this occasion we were able to fly the Society's Flag from one of our windows as a part of the decorations of Burlington House. This flag, which had been discovered by the Society of Antiquaries among their ' Lares et penates ' had been returned to us a few weeks previously. Among the Honours conferred by Her Majesty to celebrate her Coronation, she was graciously pleased to confer upon me, as your President, the Coronation Medal.

As your President I have attended during the past year a number of functions of various kinds :—

On 1 July, I presided at the unveiling of a Plaque on the house in Broadstone, Dorset, which Dr. Alfred Russel Wallace had built and in which he died : associated with me were Sir Charles Evans, F.R.S., representing the Royal Society and Dr. Edward Hindle, F.R.S., representing the Royal Geographical Society. We were accompanied by Mr. H. E. Clark and Mr. Henry Bury, a Fellow and former Member of Council of this Society, who represented the Bournemouth Natural Science Society, and by Dr. G. D. Drury, the representative of the Dorset Natural History and Archaeological Society. The actual unveiling was performed by Alderman Miss Llewellyn, the Mayor of Poole, in whose jurisdiction Broadstone lies, and it was a great pleasure to have with us Dr. Wallace's daughter-in-law and his two grandsons, as well as several friends who had known Dr. Wallace during his residence in the town. After the ceremony we proceeded to the cemetery and laid a wreath on his grave. We were then entertained to tea by Mr. Carter, the Chairman of the Poole

Pottery Works, which made the plaque, and his wife. On this occasion I was accompanied by our Zoological Secretary, Dr. Tindall Hopwood, and our thanks are due to Mr. Guy Otter, F.L.S., who made the local arrangements, and finally to Brigadier-General Tyndale-Biscoe for granting permission for the plaque to be affixed to the house, which he now owns.

On 20 August I had the honour to represent the Society as their delegate at the meeting of the International Congress of Limnology in Cambridge ; and on 22 March I had the honour to represent the Society at the Bicentenary Celebrations of the Royal Society of Arts and to present to their Chairman of Council, Lord Radnor, our Address of Congratulations and Good Wishes.

On 6 February, by permission of your Council, I had great pleasure in leading a Deputation, composed of Dr. C. F. A. Pantin, Dr. John Smart and myself from the Society, to congratulate Mr. Cyril Warburton on attaining his 100th birthday. Mr. Warburton is not a Fellow of this Society but he is well known to all arachnologists as an expert on spiders, and to me personally, as he is a Member of my own college, Christ's College, Cambridge, and many years ago demonstrated to me, when I was a young student studying parasitology.

Our Treasurer, Col. F. C. Stern, represented the Society at the Centenary Celebrations of the Brighton and Hove Natural History Society and presented a letter of congratulation from us.

In July, I hope to represent the Society as your delegate at the Sesqui-Centenary Celebrations of the Royal Horticultural Society ; and our Botanical Secretary, Dr. George Taylor, will represent the Society at the VIIIth Meeting of the International Botanical Congress to be held in Paris.

A letter of greetings was sent to Italy on the occasion of the celebration on 27 March of the centenary of the birth of Batista Grassi, one of the pioneers in the discovery of the connection between malaria and the mosquito.

Our Library continues to expand and during the past year we have added five institutions to our Exchange List, and we have become an Associate Member of the International Association for Plant Taxonomy. Like other Scientific Libraries we are faced with the problem of maintaining our purchases of foreign, and particularly German, publications owing to the greatly increased cost. In order to investigate what could be done to maintain the availability of such publications a meeting, at which I presided, of the Librarians of most, if not all, of the main London libraries was held in our rooms. The first step was to compile a list of all the publications that are taken by the different libraries : this I believe has been done, and it now remains to study the question whether arrangements could be made whereby the different libraries should take certain publications and make them available for consultation to scientists of other bodies, so that in some such way unnecessary duplication might be avoided. It is hoped that it will be possible to hold another meeting at some time during the summer. Our Library continues to be in considerable demand and during 1953 the National Central Library borrowed 680 volumes from us : this number was only exceeded by the number borrowed from the Science Museum Library and the library of the London School of Tropical Medicine and Hygiene. Dr. A. H. Uggla, of Sweden, has continued to work in the Society's rooms on the compilation of a catalogue of the Linnean MSS., which we hope to publish in the not too distant future. Dr. Uggla is already an Associate *honoris causa* of the Society and in recognition of his work he has now been recommended by the Council for election to Foreign Membership of the Society.

Our Librarian, Mr. W. S. Warton, has been absent, owing to illness, since the Christmas recess : he suffered from a ' stroke ' : it seems very doubtful if he will ever be able to return to duty, and one of the first duties of the Council will be to try to find someone who will take his place. In the meantime our caretaker, Mr. Wislawski, who has a knowledge of both Polish and Russian languages, has been appointed to assist our General Secretary, on whose shoulders the great bulk of the Library work has of necessity fallen, by working in the Library in the afternoons.

The Inspection Committee for the Linnaean and Smithian Collections was appointed in accordance with our Bye-Laws and an inspection was carried out for, as I understand, the first time since 1946, when the Collections were returned to Burlington House, after the last war. I am happy to inform the Society that the condition of the Collections is good and the Butterfly Collection is in admirable condition after nearly 200 years. It is proposed to make a more extended examination during the summer and thereafter to submit to your Council specific recommendations on steps that should be taken to increase the facility for the examination of the Collections by *bona fide* workers. I should like to congratulate our two Curators, Mr. N. Y. Sandwith and Mr. W. H. T. Tams, on their work and to convey to them the thanks of the Society for the care that they have taken in looking after our priceless Collections.

The President's Reception was held on 3 December and was a great success: our rooms, that were most tastefully decorated with a number of plants and young tropical trees by the London University Botanical Supply Unit, were crowded and a number of most interesting exhibits were on view and our thanks are due to the British Museum (Natural History), the Royal Botanic Gardens, Kew, the Ministry of Agriculture and Fisheries (Veterinary Laboratory), the Freshwater Biological Association, the Pharmaceutical Society of Great Britain and the Cambridge Botanic Garden, as well as to several Fellows of the Society. A most interesting colour and monochrome film on 'Under-water Cine-Photography in the Ocean' was shown with a running commentary by Mr. W. Deryck Chesterman, of the Royal Naval Scientific Service. To all who contributed to the success of the Reception I tender my most grateful thanks.

As in previous years the Rooms of the Society continue to be used on many occasions for Committees and Meetings of kindred Societies.

During the year the following publications were issued :—

The Journal—Botany, No. 356,
Proceedings of our 164th Session, Part 2, and
Synopsis No. 9 on Woodlice.

It was hoped that our *Proceedings* for the 165th Session, Part 1, and the Zoological number of the *Journal* would be published before this Meeting but unfortunately publication has been delayed.

I have been asked by the Trustees of the Murdoch Trust to bring this Trust to the notice of the Fellows of this Society. The Murdoch Trust is a scheme for " the Relief of Indigent Bachelors and Widowers who have shown practical sympathy in the Pursuit of Science ". The Trust awards annual grants or pensions and the applicant must be of not less than 55 years of age.

Finally, our thanks are due to our two Secretaries, Dr. Tindell Hopwood and Dr. George Taylor for the work that they have done for the Society during the past year, and last, but by no means least, to our Treasurer, Col. F. C. Stern, who has looked after our finances with the great care that we have learned by past experience to expect from him, in spite of the fact that his *alter ego* as Master-Warden of the Drapers Company has entailed his absence from some of our Council Meetings. Our sincere thanks are also due to our salaried Staff, our General Secretary, Mr. T. O'Grady, and our Clerk, Mrs. Edith Ziegler, for the efficient manner in which they have carried out their duties.

TREASURER'S REPORT

Printed copies of the accounts for the financial year which ended on 30 April 1954 are before you. For comparison, the figures for last year are printed in italics on the left-hand side. A statement has been prepared by the Auditors who certify as to details; the Audit Committee has inspected the books, verified the investments and bank balance and passed the accounts; the action of the Committee has been confirmed by the Council.

I will briefly go through the accounts and deal with the main items :—

On the Income Side.

The Annual Contributions and arrears are slightly higher than last year due to more arrears having been paid.

Annual Contributions under Deeds of Covenant.

It will be seen that we received £348 in refund of Income Tax on Deeds of Covenant signed by Fellows. These Covenants are a great help to the finances of the Society and it is very much hoped that as many Fellows as possible will sign this Covenant which will make no difference to their income but will make a great difference to the income of the Society. Deeds of Covenant can be obtained from the General Secretary.

The Sales of Publications are the highest we have had for many years, which is due no doubt to their excellence but also due to the Society selling the publications direct and not through an agent. I should like to say how much we are indebted to our General Secretary for making these arrangements.

The Society received through the Royal Society the sum of £950 from the *Parliamentary grant-in-aid for Publications.* We are deeply grateful for this help to our funds for expenditure on Publications. The Society has paid the whole of the cost of publications up to date which includes all those publications which have been issued this year or will be issued in the near future.

I should like to say a word now with regard to the finance of Publications which is such an important side of the work of the Society.

It will be noticed on the payment side that the amount spent on publications this year has been £1,366 as against £2,459 in the previous year.

In the year 1952–53 two *Journals, Zoology* and one *Journal, Botany* were published, also four parts of the *Proceedings.*

In 1953–54, one *Journal, Botany* and one part of the *Proceedings* have been published, also one *Synopsis.*

There has been a delay in publication of the *Journal, Zoology,* and no doubt next year two *Journals, Zoology* will be published and three parts of the *Proceedings.*

The Council have put aside £900 from this year's account to the Publication Reserve Fund which will help to pay for the extra publications to be issued in the coming year.

The Publication Reserve Fund last year stood at £2,490 which included the Auckland University grant of £500 for Prof. Chapman's Algae paper; this has now been shown separately, in order that the Reserve Fund made by the Society for publication can be clearly seen. The Fund now stands at £2,890 which consists of the £2,490 less £500 Auckland University grant plus £900 which we have been able to put to Publication Reserve from the accounts of the year just ended.

TREASURER'S ACCOUNTS FOR THE

(Presented at the Anniversary

Receipts and Payments of the Linnean Society

General

1952–53 £	RECEIPTS	£	s.	d.	1953–54 £	s.	d.
	To Balance at 1 May 1953 :—						
	Current Account at Bank	214	6	7			
	Deposit Account Post Office Savings Bank	320	12	2			
	Cash in hand	16	3	2			
	Awaiting Investment	144	0	0			
515					695	1	11
80	,, Admission Fees				76	0	0
	,, Arrears of Annual Contributions	126	4	9			
	,, Annual Contributions for year	2759	6	10			
	,, in advance	102	2	3			
2857					2987	13	10
25	of Associates				27	19	0
217	,, Inland Revenue on Deeds of Covenant				348	7	2
80	,, Composition Fees				81	0	0
367	,, Interest and Dividends (including Income Tax recovered)				423	16	4
118	Post Office Savings Bank Account				116	4	6
	,, Sales of Publications :—						
	Transactions	174	13	6			
	Journals	544	1	1			
	Proceedings &c.	259	12	4			
575					978	6	11
	,, Grants in aid of Publications :—						
1250	Royal Society	950	0	0			
—	Prof. J. McLean Thompson	15	0	0			
10	*Dr. C. F. A. Pantin*	—					
500	*Auckland University*	—					
293	*Dr. Hugh Scott*	—					
—	Mr. J. D. Snowden	25	0	0			
					990	0	0
42	,, Miscellaneous Receipts				126	15	2
746	,, *Transfer from Reserve for Publications Fund*				—		
£7675					£6851	4	10

Library

£		£	s.	d.
209	To Balance at 1 May 1953	199	8	8
79	,, Interest on Investments (including Income Tax recovered)	79	2	7
10	,, Donation : John Innes Horticultural Institution	10	0	0
300	,, Transfer from General Account	300	0	0
—	,, Gift in Memory of Miss Maud Williams	100	0	0
—	,, War Damage Settlement on F. Druce Bequest	58	0	10
£598		£746	12	1

Library

£		£	s.	d.
1036	To Balance at 1 May 1953	869	11	11
17	,, Donations : Fellows and Friends	18	3	0
	Interest on Deposit Account	15	11	10
£1053		£903	6	9

Fellows' Postal

£		£	s.	d.
50	To Balance at 1 May 1953	50	6	5

YEAR ENDED 30 APRIL 1954

Meeting, 24 May 1954)

from 1 *May* 1953 *to* 30 *April* 1954

Account

1952–53 £	PAYMENTS	£	s.	d.	1953–54 £	s.	d.
251	By Coal, Electric Current, and Gas				226	9	3
423	,, Furniture and Repairs : Sundry				468	16	7
93	,, Taxes and Insurance				91	8	8
411	,, Miscellaneous Printing and Stationery				320	1	7
360	,, Petty Expenses and Postages				428	0	2
	,, Publications :—						
	Printing	1232	14	10			
	Distribution	44	4	5			
	Illustrations	89	2	10			
2459					1366	2	1
993	,, Transfer to Reserve for Publications Fund				900	0	0
1520	,, Salaries, Wages and Pension				1645	2	8
15	,, ‘ Zoological Record ’ (Vol. 89) Donation				15	0	0
10	,, *William Wright Smith Lecture Fund*—Donation				—		
2	,, *International Union for Nature Protection*—Donation				—		
108	,, Staff Annuities (Annual Premiums)				108	0	0
—	,, Investment of Compounders' Fees				144	0	0
35	,, Linnean Medal				31	2	6
300	,, Transfer to Library Account				300	0	0
	,, Balance at 30 April 1954 :—						
	Current Account at Bank	89	16	9			
	Deposit Account at Bank	100	0	0			
	Deposit Account Post Office Savings Bank	436	16	8			
	Cash in hand	15	7	11			
	Amount awaiting Investment	165	0	0			
695					807	1	4
£7675					£6851	4	10

Account

£		£	s.	d.	£	s.	d.
206	By Periodicals				212	0	4
174	,, Binding				252	4	6
18	,, Books				107	14	0
	,, Balance at 30 April 1954 :—						
	Current Account	24	13	3			
	Deposit Account Post Office Savings Bank	150	0	0			
200					174	13	3
£598					£746	12	1

Restoration Fund

£		£	s.	d.	£	s.	d.
183	By *Carpet for Library*				—		
	,, Balance at 30 April 1954 :—						
	Current Account at Bank	40	10	5			
	Deposit Account at Bank	46	2	4			
	Deposit Account Post Office Savings Bank	816	14	0			
870					903	6	9
£1053					£903	6	9

Account

£		£	s.	d.
50	By Balance at 30 April 1954	50	6	5

Special Accounts
(Trust and Reserve Funds)

RECEIPTS

	£	s.	d.	£	s.	d.
To Balance at 1 May 1953 :—						
Westwood Fund	147	5	2			
Trail Award Fund	29	10	6			
Crisp Award Fund	41	17	1			
Hooker Lecture Fund	174	15	8			
Goodenough Fund	34	18	8			
Minchin Fellowship Fund	16	10	5			
Carnegie Corporation Grant	419	3	7			
Reserve for Publications Fund	2490	5	3			
Deposit (Dr. A. H. Uggla)	15	0	0			
				3369	6	4
,, Transfer from Reserve for Publications Fund				900	0	0
,, Interest on Investments (including Income Tax recovered) :—						
Westwood Fund	10	17	4			
Trail Award Fund	3	11	6			
Crisp Award Fund	13	19	0			
Hooker Lecture Fund	21	18	0			
Goodenough Fund	8	12	9			
Minchin Fellowship Fund	3	0	0			
Staff Pension Fund	9	9	9			
				71	8	4
				£4340	14	8

PAYMENTS

	£	s.	d.	£	s.	d.
By Repayment to Dr. Uggla				15	0	0
,, Staff Pension Fund :—						
Purchase of £9 16*s.* 1*d.* 3 per cent Savings Bonds 1955–65				9	9	9
,, Balance at 30 April 1954 :—						
Westwood Fund	158	2	6			
Trail Award Fund	33	2	0			
Crisp Award Fund	55	16	1			
Hooker Lecture Fund	196	13	8			
Goodenough Fund	43	11	5			
Minchin Fellowship Fund	19	10	5			
Carnegie Corporation Grant	419	3	7			
Reserve for Publications Fund	2890	5	3			
Auckland Univ. Grant (Chapman)	500	0	0			
				*4316	4	11
				£4340	14	8

* Including £3362 11*s.* 2*d.* in Post Office Savings Bank.

£	s.	d.	*General Account*		Market value 30 *April* 1954. £	s.	d.
1000	0	0	3½ per cent London County Consolidated Stock 1958–68	@ 98	980	0	0
1548	8	9	British Transport 3 per cent Guaranteed Stock 1978–88	@ 87	1347	2	9
543	17	2	3½ per cent War Loan, 1952 or after	@ 87	473	3	5
1000	0	0	2½ per cent Defence Bonds	@100	1000	0	0
2199	18	6	4 per cent Australian Stock 1961–64	@101	2221	18	6
200	0	0	3 per cent War Stock 1955–59	@102	204	0	0
1139	13	0	3 per cent Savings Bonds 1955–65	@ 97½	1111	3	2
3260	1	3	2½ per cent Consolidated Stock	@ 66½	2167	18	10
176	19	3	3 per cent Savings Bonds 1960–70	@ 93	164	11	6
274	5	5	3 per cent Treasury Stock	@ 78	213	18	8
176	2	11	3½ per cent War Loan 1952 or after	@ 87	153	4	1
					£10037	0	11

£	s.	d.	*Library Account*		£	s.	d.
471	18	9	British Transport 3 per cent Guaranteed Stock 1978–88 (Bentham Bequest)	@ 87	410	11	8
103	12	5	Surrey County 3 per cent Stock 1961–66 (Wakehurst Bequest)	@ 94	97	8	1
191	12	7	4 per cent Australian Stock 1961–64 (Walker & Morey Bequests)	@101	193	11	0
107	2	1	2½ per cent Consolidated Stock (Stebbing Bequest)	@ 66½	71	4	10
530	0	0	3 per cent Savings Bonds 1960–70 (Tagart Bequest)	@ 93	492	18	0
1414	7	11	2½ per cent Consolidated Stock (Flintoff Bequest)	@ 66½	940	11	5
					£2206	5	0

	£	s.	d.	*Special Accounts*		£	s.	d.
£1063 10 7	232	5	0	Metropolitan Water Board 3 per cent " B " Stock (Westwood Bequest)	@ 81	188	2	5
	667	14	2	,, ,, (Hooker Lecture Fund)	@ 81	540	16	10
	163	11	5	,, ,, (Goodenough Fund)	@ 81	132	9	10
	557	12	1	2½ per cent Consolidated Stock (Crisp Award Fund)	@ 66½	370	16	1
£380 10 6	156	7	2	,, ,, ,, (Westwood Fund)	@ 66½	103	19	7
	74	14	6	,, ,, ,, (Hooker Lecture Fund)	@ 66½	49	13	10
	149	8	10	,, ,, ,, (Goodenough Fund)	@ 66½	99	7	7
	313	18	9	3 per cent Savings Bonds 1955–65 (Staff Pension Fund)	@ 97½	306	1	8
	9	16	1	,, ,, ,, 1955–65 (Staff Pension Fund)	@ 97½	9	11	2
	100	0	0	,, ,, ,, 1960–70 (Minchin Fund)	@ 93	93	0	0
	102	3	11	3½ per cent War Loan 1952 or after (Trail Award Fund)	@ 87	88	18	3
				F. C. STERN, *Treasurer.*		£1982	17	3

We have (in conjunction with the Professional Auditors, who certify as to all details) audited the Accounts of the Society for the year ended 30 April 1954 and found them correct. We have verified the Investments and Bank Balances.

19th May 1954.

W. B. KEEN & Co., *Chartered Accountants,*
Finsbury Circus House,
Blomfield Street, London, E.C.2.

F. L. BALFOUR-BROWNE
MARGARET A. P. MADGE
ALAN FISK

R. B. SEYMOUR-SEWELL
GEORGE TAYLOR
E. W. BAXTER
} *Audit Committee.*

On the Payment Side.

Coal and Electric Current, and Gas has cost less owing to the warm autumn.

Furniture and Repairs are high owing to the redecoration of the staircase and second-floor hall. Also a new carpet has been put in the Meeting-Room Annex, and the chairs in that room have been completely repaired. One of these chairs which belonged to Robert Brown is a valuable possession of the Society. The Society has also bought a new 2×2 projector for showing coloured photographs and also a new and most useful apparatus for photographing manuscripts, from which we hope to derive some income.

Printing costs have remained fairly stationary.

Salary, Wages and Pensions are much the same as last year.

Library Account.

The Account has a balance of £174 after paying the usual items.

Library Restoration Fund.

This Fund now has a balance of £903 out of £3,420 which has been subscribed. The binding and repairs to books since first it was formed, amount to about £1,367 ; the purchase of foreign works that were missing in our sets £374, and extra shelving has cost £610.

The Society has received only £18 towards this fund this last year. I should like again to appeal to all friends of the Linnean Library to help this Fund, which I think is extremely important, in any way they can by donations or by legacies, in order that this historic and valuable Library can be maintained and conserved as it should be.

Trust and Reserve Fund.

I have already mentioned the Publications Reserve, and there is no more to report on the Trust and Reserve Funds, except that we refunded to Dr. Uggla of Uppsala £15 deposited by him during an earlier visit.

Investments. £144 Composition Fees has been invested in £176 2*s*. 11*d*. 3½ per cent War Loan.

I should like to thank our General Secretary, Mr. T. O'Grady and our Clerk, Mrs. Edith Ziegler, for the excellent way in which the accounts have been kept, and for the conscientious way in which the work has been done.

If any Fellow wishes to ask any questions on these accounts, I will do my best to answer them.

On a motion by Dr. B. BARNES, seconded by Dr. L. HARRISON MATTHEWS, F.R.S., the Report and Statement of Accounts were adopted.

The PRESIDENT then delivered his Address on " The Continental Drift Theory and the Distribution of the Copepoda ". **[Printed in full on p. 149.]**

On its conclusion, Dr. JOHN RAMSBOTTOM, O.B.E., moved " That the President be thanked for his excellent Address, and that he be requested to allow it to be printed and circulated amongst the Fellows ". The motion was seconded by Mr. I. H. BURKILL, and being put to the meeting was carried with acclamation.

The President announced that he had appointed the following as Vice-Presidents for 1954–55 :—Professor C. T. Ingold, Dr. C. F. A. Pantin, F.R.S., Professor J. E. Smith and Colonel F. C. Stern, O.B.E., M.C.

Thereafter the President declared the Session of 1953–54 closed.

ADDITIONS AND DONATIONS TO THE LIBRARY

1953–54

Note.—Names of donors are given in square brackets. Separate copies of papers which are included in periodicals received by the Library are no longer catalogued.

Abercrombie, John. *See* **Mawe, Thomas.**
Adamson, R. S., & Salter, T. M., *edited by*. Flora of the Cape Peninsula. Pp. xix+889. 8vo. *Cape Town*, 1950.
Andrews, F. W. The Flowering Plants of the Anglo-Egyptian Sudan, Vol. 2. Pp. viii+486. (Sterculiaceae-Dipsacaceae). 8vo. *Arbroath*, 1952.
Arber, Agnes. The Mind and the Eye. A study of the Biologist's standpoint. 8vo. *Cambridge*, 1954. [Author]
Baileya. A Quarterly Journal of Horticultural Taxonomy. Vol. 1. → 1953 →
Baker, Henry. The Microscope made easy. Pp. 324. 8vo. *London*, 1769.
Beddows, A. R. The Ryegrasses in British Agriculture : a Survey. Pp. 82. 8vo. *Aberystwyth*, 1953. [Author.]
Binz, Auguste, & Thommen, Edouard. Flore de la Suisse. Pp. xxxvi+450. 8vo. *Lausanne*, 1953. [E. Thommen.]
Bock, Thor Methven. *See* **Marshall, W. Taylor.**
Boerman, A. J. Carolus Linnaeus als middelaar tussen Zweden en Nederland (with a Summary in English). Pp. 208+xxiv. 8vo. *Utrecht*, 1953. [Author.]
Bond, T. E. T. Wild Flowers of the Ceylon Hills. Pp. xviii+240. 8vo. *Madras*, 1953. [Author.]
Bonner, John Tyler. Morphogenesis. Pp. 296. 8vo. *Princeton*, 1952.
Borlase, William. The natural history of Cornwall. Pp. xviii+328. Fol. *Oxford*, 1758.
British Journal of Animal Behaviour, The. Vol. 1. → 4to. *London*, 1953. →
British Museum (Natural History).
  Conisbee, L. R. A list of the names proposed for Genera and Sub-genera of Recent Mammals. Pp. 109. 8vo. *London*, 1953.
  Ellerman, J. R., Morrison-Scott, T. C. S. and Hayman, R. W. South African Mammals. 1758–1951. A reclassification. 4to. *December*, 1953.
  Evans, W. H. A catalogue of the American Hesperiidae, indicating the classification and nomenclature adopted in the British Museum (Natural History). Pp. v+178. 8vo. *London*, 1952.
  Smout, Alan Hilder. Lower Tertiary Foraminifera of the Qatar Peninsula. Pp. ix+96. 8vo. *London*, 1954.
  An illustrated catalogue of the Rothschild collection of Fleas (Siphonaptera) in the British Museum (Nat. Hist.). By G. H. E. Hopkins & Miriam Rothschild. Vol. I. Tungidae & Pulicidae. Pp. xvi+362+45 pls. 4to. *London*, 1953.
  The Trichoptera (Caddis Flies) of Australia and New Zealand, described and figured by M. E. Mosely & D. E. Kimmins. Pp. 550. 8vo. *London*, 1953.
  A monograph of the immature stages of British and imported Timber Beetles. (Cerambycidae). By E. A. J. Duffy. Pp. viii+350+8 pls. 8vo. *London*, 1953.
  Catalogue of Fossil Cirripedia in the Department of Geology. Vol. III. Tertiary. By T. H. Withers. Pp. xvi+396+64 pls. 8vo. *London*, 1953.
  Instructions for collectors. No. 3. Reptiles, Amphibians and Fishes. Ed. 6. Pp. 28. 8vo. *London*, 1953.
Brooks, F. T. Plant diseases. Ed. 2. Pp. vi+458. 8vo. *Oxford*, 1953.
Burton, Maurice. Animal Courtship. Pp. 268. 8vo. *London*, 1953. [Publishers.]
Cameron, H. C. Sir Joseph Banks. Pp. xx+342. 8vo. *London*, 1952.
Clauson, Jens. Stages in the Evolution of Plant Species. Pp. viii+206. 8vo. *Ithaca*, N.Y., 1951.
Cole, F. J. A history of Comparative Anatomy. Pp. viii+524. 8vo. *London*, 1949.

Correll, D. S. Native Orchids of North America. Pp. xvi+400. 8vo. *Waltham, Mass.*, 1950.

Cowell, M. H. A floral guide for East Kent. Pp. xiv+98. 8vo. *Faversham*, 1839.

Crane, M. B., & Lawrence, W. J. C. The Genetics of Garden Plants. Ed. 4. Pp. xviii+302. 8vo. *London*, 1952.

Croizat, Léon. Manual of Phytogeography. Pp. viii+588+105 maps and 1 figure. 8vo. *The Hague*, 1952.

Curtis, William. Practical observations on the British Grasses. Pp. 166. 8vo. *London*, 1824.

Dale, Ivan R. A descriptive list of the introduced trees of the Uganda Protectorate. Pp. iv+76. 8vo. *Glasgow*, 1954.

Dawes, Ben. The Trematoda. Pp. xvi+644. 8vo. *Cambridge*, 1946.

de Beer, G. R. Embryos and Ancestors. Pp. xii+160. 8vo. *Oxford*, 1951.

Deraniyagala, P. E. P. A Coloured Atlas of some Vertebrates from Ceylon. Vol. I Fishes. Pp. xiv+149+34 pls. Vol. II. Tetrapod Reptilia. Pp. xii+101+35 pls. 4to. *Colombo*, 1952–3. [AUTHOR.]

Dice, Lee R. Natural Communities. Pp. xii+548. 8vo. *Ann Arbor*, 1952.

Dobson, Roderick. The birds of the Channel Islands. Pp. xvi+264. 8vo. *London*, 1952.

Dobzhansky, Theodosius. Genetics and the Origin of Species. Ed. 3. Pp. xii+364. 8vo. *New York*, 1951.

Dony, John G. Flora of Bedfordshire. Pp. 532. 8vo. *Luton*, 1953.

Duffy, E. A. G. *See* **British Museum (Natural History).**

Eales, N. B. The Littoral Fauna of Great Britain. Pp. xviii+306. 8vo. *Cambridge*, 1952.

Erdtman, G. Pollen morphology and Plant Taxonomy. Angiosperms. (An introduction to Palynology. I.) Pp. xiv+540. 8vo. *Stockholm*, 1952.

Esau, Katherine. Plant Anatomy. Pp. xii+736. 8vo. *New York*, 1953. [PUBLISHERS.]

Fisher, J., & Lockley, R. M. Sea-Birds. An introduction to the Natural History of the Sea-birds of the North Atlantic. (New Naturalist Series.) 8vo. *London*, 1954. [SIR NORMAN KINNEAR.]

Gäumann, Ernest Albert. The Fungi. A description of their morphological features and evolutionary development. Pp. 420. 8vo. *London*, 1952.

Gardner, C. A. Flora of Western Australia. Vol. 1, Part 1 (Graminae). 8vo. *Perth*, 1952.

Gilmore, Charles W. Fossil Lizards of North America. (Repr : Mem. Nat. Acad. of Sci.). Pp. lx+169. 8vo. *Washington*, 1928. [A. A. BULLOCK.]

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BENEFACTIONS

LIST *in accordance with Bye-Laws, Chap.* 17, *Sect.* 1, *of all Donations of the amount or value of Twenty pounds and upwards, received during the past five years.*

1950

The Royal Society: Grant in-aid of publications, £750.
Miss E. F. Noel : Bequest of £100 for general purposes.
Mr. E. A. Robins : Long run of the Society's publications.
Mr. W. C. Barton : Long run of the Society's publications.
Mrs. E. W. Sexton : Donation towards the cost of the joint paper on *Jassa* in the *Journal, Zoology*, £50.

1951

The Royal Society : Grant-in-aid of publications, £750.
Mr. James Insch, F.L.S. : Bequest of Library of works on Tea.
Mr. John H. Robins : The collected correspondence of Richard Pulteney, F.R.S., F.L.S.

1952

The Royal Society : Grant-in-aid of publications, £1250.

1953

Auckland University College : Grant towards cost of Prof. V. J. Chapman's paper on New Zealand Algae in *Journal, Botany* (press), £500.
The Royal Society : Grant-in-aid of publications, £950.
Mr. J. D. Snowden : Gift towards cost of paper on *Sorghum* in *Journal, Botany* (press), £25.
Gift to Library Fund in Memory of Miss Maud Williams, F.L.S., £100.
Dr. Hugh Scott, F.R.S. : Cost of blocks for plates and £293 0*s*. 11*d*. towards cost of printing his Gughé Highlands' paper in *Proceedings*, **163**.

1954

Mr. H. Womersley, A.L.S. : Gift towards cost of paper in *Journal, Zoology*, No. 288, £20.
Imperial Chemical Industries Limited : Gift to Library Fund, £21.
The Royal Society : Grant-in-aid of publications, £1000.
Mr. A. A. Pearson, F.L.S. : Bequest of Myological Library.

OBITUARIES

In Dr. **George Parker Bidder** British zoology has lost one of its best known followers, one to whom zoologists have for many years and in many ways owed a very great deal and to whom they have been accustomed to turn for advice and help. In him, also, the Society has lost a fellow of long standing who had served it in many ways.

George Parker Bidder was born in 1863 the son of an eminent barrister of the same names who was largely engaged in parliamentary litigation in the middle of the nineteenth century. His grandfather, after a youth at the beginning of the century as a mathematical prodigy, was responsible as engineer for the planning of the North-Western railway over Shap, and for much other work in the building of railways in this country and abroad. In this he was associated with Robert Stephenson and his firm. Perhaps the width of Dr. Bidder's interests, as shown in his publications extending over art, poetry—he published two volumes of poems—archaeology, geology, as well as all branches of biology, owed something to this ancestry.

Dr. Bidder was educated at Harrow. After leaving school in 1881, he spent a year at University College, London, studying zoology under Ray Lankester, whose inspiration he always in later life regarded as having been of the greatest value to him. Here also he met J. T. Cunningham who, shortly after leaving Oxford, had taken a post in Lankester's department. This was the beginning of a friendship which continued through many later years when they were both working at the Plymouth laboratory. Dr. Bidder went up to Trinity College, Cambridge, in October 1882, as an exhibitioner in mathematics and science. It was in this year that F. M. Balfour was made Professor of Animal Morphology, and it was also in the summer of this year that Balfour died as the result of an accident in the Alps. Dr. Bidder therefore did not come directly under Balfour as a teacher, but there can be no doubt that Balfour's influence dominated the department for many years after his death. It has indeed been said that it was Balfour's ghost that ruled the department in those days. Under this influence Dr. Bidder received the greater part of his zoological training from Newton, Sedgwick, Harmer, Weldon, Gadow and other members of the department. When he died he was almost the last representative of the Cambridge zoologists of the 1880's. Mr. Cecil Warburton still remains but probably no-one else. Dr. Bidder gained a first class in the Natural Sciences Tripos Part I in 1884 and a second class in Part II in 1886. He graduated B.A. in 1886 and M.A. in 1895.

Being financially independent, he was able to devote himself to his biological interests as soon as he had completed his course at Cambridge. He spent most of the next few years working on sponges at Plymouth, Naples and Cambridge. At Naples he occupied the University Table in 1886 and 1888, and there, in 1889, he bought the hotel which he renamed Parker's and owned until 1922, managing it for some years himself. Both at Plymouth and Naples he did a great deal to support the laboratories. An account of the early days at Plymouth is contained in his obituary of E. J. Allen (*J. mar. biol. Ass.* **25,** 1943) and fuller accounts of it are given in the obituary of Dr. Bidder published in that journal. Here it need only be said that he was one of the most active in forwarding the development of the laboratory in the first twenty years of its life, and that he continued to do so until the end, being on the Council of the M.B.A. from 1899 and its President from 1940 to 1944.

In 1899, Dr. Bidder married Miss Marion Greenwood, a Fellow of Newnham and a physiologist. He then set up his home at Cavendish Corner, Cambridge, so well known to succeeding generations of zoologists. They had two daughters, one of whom Miss Anna Bidder is now a Fellow of the Society, and at the time of his death he had three grandchildren. Mrs. Bidder died in 1932.

* *J. mar. biol. Assn.* **34,** 1, 1955, where a list of his publications is included.

In 1905, Dr. Bidder was obliged to retire for some time from active work and go to various sanatoria for treatment of an infection which had been developing for some years. His cure was not complete until after the 1914–18 war, for he had a recurrence during the war brought on by work which he undertook for the Admiralty and in which he overtaxed himself. He was, however, in the years immediately before the war (1910–14) able to make observations on the geology of the Norfolk coast, and on the bottom currents of the North Sea as shown by the movements of trailer bottles. After the war he was able to take up again his biological work and his many other interests.

It is not possible in this notice to detail all Dr. Bidder's activities in the latter part of his life. He was given the Sc.D. degree by the University of Cambridge in 1916, and lectured on sponges in the course for Part II of the Tripos from 1920 to 1927. The present writer attended that course and well remembers his skill in bringing out the biological interest of the group, not the easiest to make interesting to students. He promoted the Company of Biologists Ltd. in 1925 as a means of providing financial support for biological journals, and was its secretary from 1925 to 1928. He was President of Section D of the British Association at Hull in 1927, when he read his paper on the ' Ancient History of Sponges and Animals '. With Professor Balfour Browne he founded the Association of British Zoologists, and was its Chairman at the annual meetings in 1927 and 1928. One of his most outstanding services to zoology, though less public, was the financial support that he gave to the *Quarterly Journal of Microscopical Science* through many years; he was in fact the owner of the journal, taking the financial risks of its publication. In addition, he was during all these years active in business. He was for many years a director of his family firm, the Cannock Chase Colliery Company, and, for a period, its managing director.

Throughout his life Dr. Bidder's chief zoological interest was the biology of sponges, and with that group of animals all his more important contributions were concerned. When one re-reads his papers, one is struck with the breadth and modernity of his outlook even in the earliest papers. Sponges were to him subjects in natural history, living animals, and his object was to understand their life and the means by which it is maintained. To this end he made use of any scientific method of investigation that could be useful. Comparative anatomy, histology, observation and growth of specimens under experimental conditions, and mathematical analysis were all at some stage brought in to help the progress of the investigation. This was his outlook from the start. He was, for instance, able to say at the beginning of his paper on ' The Relation of the Form of a Sponge to its Currents ', published in the *Quart. J. micr. Sci.* **67**, 1923, that a preliminary note dealing with the same subject had been published in *Proc. Camb. Phil. Soc.*, 1888. That was, in fact, his earliest paper and reference to it shows that much of the theory developed in the later paper was already in his mind.

From the start of his work to 1900 he was chiefly concerned with the functioning of the collar cells in producing the current of the sponge. This required accurate description of the living cells and their collars and his published papers contain much histology. There is no doubt that this work has stood the test of time, as for instance in his disproof of the real existence in normal conditions of Sollas' membrane. On these mainly histological papers, his later work on the biology of sponges was based. His earlier papers also contain many observations on the amoebocytes, reproductive cells and other constituents of the sponge body.

After his illness he was able to put together and extend the conclusions to which his earlier work had led. In 1923 he read to the Society and published the paper already mentioned on the forms of sponges. In it he showed, with the help of considerable mathematical analysis, the close adaptation of the structure of the sponge to efficiency in producing a feeding current of clean water. He proved not only that the size of the osculum is accurately adjusted to this purpose, but also that the forms of sponges in different habitats are correlated with such features of the habitats as the currents in them and the nature of the substratum. In 1927 his address to Section D of the British Association was concerned with the question whether sponges should be regarded as ancestral to other multicellular animals. In 1930, he discussed before the Society the part played by Brownian movement in the uptake of food by the collar cells, again with the help of mathematical analysis. Finally, in 1937, he read before the Society his paper on ' The Perfection of Sponges ', in which he returns to discussion of the adaptation of the sponge to the conditions of its life, pointing out that the perfection of their adaptation has enabled them to survive through the whole of palaeontological time without essential modification.

These were Dr. Bidder's more important papers, but he also published many shorter contributions on various subjects, and was always active in discussion at the Society's meetings.

All his work shows him to have been a biologist interested in the biology and natural history of sponges, a biologist who realized the necessity of making use of every available scientific method in the study of his organisms. If ecology is no more than scientific natural history, and that is perhaps its most accurate description, Dr. Bidder may be said to have been a pioneer of zoological ecology, a pioneer whose outlook anticipated by many years views widely held today. But this does not completely describe his work. To him a large part of the attraction of natural science lay in what he called ' imaginative speculation '. Speculation might sometimes lead one astray, but he held that it was nevertheless essential for the advance of science. His papers show the use he made of it.

Dr. Bidder was elected a Fellow of the Linnean Society in 1919. He served on the Council from 1922 to 1926 and from 1927 to 1932. He was a Vice-president in 1924–5. From 1928 to 1931 he was the Zoological Secretary of the Society. It was in this last capacity that his most important work for the Society was done.

When he became Secretary, he felt that the Society was over-balanced on the botanical side and was not making the appeal that it should make to the younger zoologists. He thought of it as a meeting-place for biologists of all kinds, and he regarded the meetings as giving ideal opportunities for immediate presentation of original observations. They should, he thought, provide researchers with an opportunity of giving an outline of their problems and the methods they were using to solve them. They should also enable biologists to discuss their problems with workers in cognate fields of other branches of biology. He maintained that in London there is no other place where these needs can be so conveniently and effectively met, but if it is to succeed in doing this it is clear that the Society must appeal to all workers in biology.

He felt that so far as zoology was concerned the Society had not in the years then recent succeeded in providing this forum for all biologists, and particularly for the younger of them, and he set out to provide it by widening the zoological appeal of the meetings. He did so by asking the younger zoologists to give immediate accounts of their results, by arranging for discussions on subjects of general interest, and by making sure that as wide as possible a range of zoological interest was represented at the meetings. There is no doubt that he succeeded in attracting to the Society much more interest among zoologists than they had previously shown. His years as secretary were, in fact, important in the history of the Society.

In all this, Dr. Bidder had the support of Sir Sidney Harmer, then President, of Dr. Ramsbottom, the Botanical Secretary, and of other members of the Council. His own charm of manner and wide knowledge of the zoologists of the country made him an ideal person to carry out his aims. But the Secretaryship of the Society is by no means a sinecure ; it demands hard work in the preparation of the programmes for the meetings and in editing the *Proceedings* and the *Journal.* For Dr. Bidder it also meant much work in forwarding the special aims he had set for himself. After three years as Secretary, he felt that his health would no longer allow him to continue this work and he resigned. The Society has cause to be sincerely grateful to him for the guidance he gave to it and the work he did for it as secretary at that time, when he was already approaching his seventieth year. After resigning he continued to be frequently present at the meetings and to be an active member of the Linnean Club ; his contributions to the discussions and the paper he read in 1937 were no less stimulating than his earlier contributions. He died on 31 Dec. 1953.

In this account of Dr. Bidder's work for the Society I have been greatly helped by Dr. J. Ramsbottom who has given me the benefit of his memory of the time when he and Dr. Bidder were the Society's secretaries.

G. S. CARTER.

Dr. **Prabhat Chandra Sarbadhikari** was born in Bhagalpur, India, on the 1 February 1898. Before he graduated, he lost his only brother, his father and his mother in quick succession. In spite of the tremendous odds against him, he carried on courageously and after passing the M.A. examination from the Presidency College, Calcutta, he secretly proceeded to the United Kingdom. This opened a new chapter in his life, a chapter high-lighted by brilliant academic results.

In England he carried out difficult cytological work under Sir John Farmer and Prof. V. H. Blackman in the Imperial College of Science and Technology, and was a Royal College of Science Research Scholar working under Prof. John Farmer and Miss Lattice Digby. Whilst at the Imperial College he became the first Asian recipient of the coveted Huxley Memorial Gold Medal and Scholarship. He was also awarded the Marshall Prize and Scholarship, the Dixon Prize and Scholarship and the Carnegie Scholarship. His amazing capacity for original investigation won for him a prominent place in biological science and his extensive researches on the Cytology of the Osmunda and Doodia and a new Differential Method of Staining the Nucleolus are of outstanding importance. Both the papers that he submitted for his Doctor's Degree earned high acclaim from his teachers enabling him to obtain a double doctorate in Science from the University of London. He also obtained a Diploma of the Imperial College of Science, and was a Fellow of The Linnean Society of London, in 1931.

In order to obtain a first-hand knowledge of the Classification of Plants and the methods of identifying unknown species, he worked in the Herbarium of the Royal Botanic Gardens, Kew, under Sir Arthur Hill and the Dahlem Botanical Gardens, Berlin. He also studied modern horticultural methods at Wisely and at John Farmer Horticultural Institute, Merton, England, under Prof. Bateson.

In 1925 he was appointed Lecturer in Botany, University College, Colombo, by the Secretary of State for the Colonies. Subsequently he held the Chair of the Botany Department of that University. Dr. Sarbadhikari had the honour of being elected to represent Ceylon at (1) The Fifth International Botanical Congress, Cambridge, (2) Ninth International Horticultural Congress, London, (3) Conference on Fruit Production, London, (4) Imperial Botanical Conference, London, (5) Linnean Society Sesqui-Centenary, London, (6) Indian Science Congress, Silver Jubilee. He was also sent as a delegate to the Congress of the Universities of the Empire, British Association for the Advancement of Science Meeting and the Academy of Science, London and Paris in 1926. Before his appointment in Ceylon, he worked in the Botanical Laboratory in the University of Paris under Prof. Guillermond.

In 1947 he retired from Ceylon and joined the Calcutta University as Sir Rashbehari Ghose Professor of Botany and Head of the Department—a post which he held till the end.

While in India, he was elected to represent his University in connection with the Advisory Board Meetings of the Indian Council of Agricultural Research and at the Horticultural Research Worker's Conference, Madras. The Inter-University Board elected him to represent his University at the Mysore Conference, Animal Husbandry Wing of the Board of Agriculture. He guided a number of researches of Post-M.Sc. students for the Ph.D. and D.Sc. degrees and administered numerous schemes sponsored by governmental and other bodies. Dr. Sarbadhikari was connected with many educational bodies in India and abroad.

Among his many publications are those on (1) Cytology of the Osmunda and Doodia, (2) A new Differential Method of Staining the Nucleolus, (3) Cytology of Apogamy and Apospory in Osmunda Javanica, (4) Vascular system of Osmunda Cinnamamea, (5) Effects of Differential forms of Colchicine on the roots of Vicia Faba, (6) Cytological studies in the genus Ganria, (7) Apospory and Apogamy of the Doodia, (8) Importance of Fundamental Research in Food Production, (9) Fundamental Research in Plant Anatomy with special reference to the identification of crude drugs, etc. He had also served as Editor, *Ceylon Journal of Science* and the *Calcutta University Journal of Science.* He was paper-setter and examiner in the B.Sc. and M.Sc. Examination, London University, Under Grad. and Post-Grad. Classes, Ceylon University, the Ceylon Civil Service and numerous examinations in various parts of India.

As a student, he received the highest recommendation from his Professor, Sir John Farmer—the greatest Cytologist of his day, from Professor Blackman, Sir Nigel Ball, Sir Thomas Holland and many others. A conscientious teacher, he maintained good discipline though at the same time was respected and loved by all his students. He got on well with his colleagues, did not take long to establish cordial relations and always afforded loyal co-operation.

Dr. Sarbadhikari's demise was the tragic outcome of three months' severe abdominal pain and complications. For about a week before he passed away he had been doing well—but little did anyone realize that this was but the last spark of flame of a dying candle. He breathed his last at the Prince of Wales (Medical College Hospitals), Calcutta, with his beloved wife, son and daughter at his bedside—and the atmosphere rendered clean by the ringing of eventide temple bells. He was brought to his residence at 84 Ballygunge Place, Calcutta 19, and shortly afterwards taken to the Crematorium and consigned to the flames, thereby given eternal rest.

Cultured, scholarly, modest and charitable, a delightful friend and companion and a gifted and inspiring teacher, he has left a legacy of solid achievement and happy memories to those of us, who were privileged to know him.

DEV ASIS.

Mr. **James Pryde**, who was born on 18 October 1878 and became a Fellow of the Linnean Society in 1926, died at his home in Edinburgh on 7 March 1954. He was educated at Edinburgh, first at the Royal High School, and later at the University where he came under the stimulating influence of the late Professor Bailey Balfour. He retained a great respect for Bailey Balfour throughout the remainder of his life, and always spoke of him in terms of kindly affection.

Pryde's career was devoted more to education and administration than to research, but he was a painstaking investigator, and it is sad to think that most of his results will remain unknown through his failure to publish them. After leaving Edinburgh, he spent a few years in South Africa where he initiated the science departments in the High School at Kimberley. The most important part of his career was spent in India, and the writer is indebted to Professor A. Abraham, of University College, Trivandrum, who kindly supplied the following particulars.

Mr. Pryde joined the Travancore Government Educational Service in April 1911 as Inspector of Secondary Schools, and except for short periods of furlough outside India, and war service, he served for 12 years in that capacity. He was a Captain in the Indian Army Reserve of Officers during the First World War, and also assistant recruiting officer for Travancore. From 1923 to 1926 he held the additional post of Director of the Government Museum and Public Gardens. He contributed very much to the building up of a very good garden with a Zoo attached. In 1923 he was appointed Professor of Natural Science in H.H. the Maharajah's College of Science, Trivandrum. He started the present Botany and Zoology Departments of the Travancore University and was responsible for their organization. He was appointed Principal of the Maharajah's College in 1927, and returned to England, after retiring from Travancore, in 1930. Mr. Pryde was an extremely popular officer of the State Service. As Professor, and later as Principal, he commanded the respect and affection of his students and colleagues.

Mr. Pryde became known to the present writer in 1935 when he started working at the Jodrell Laboratory at Kew and he continued his investigations there until 1939. During this period he studied the chemical substances that occur in certain timbers from S. Africa and India. It is to be regretted that his conclusions, which were of considerable taxonomic as well as biochemical interest, were never published. Whilst at Kew, he also collaborated with the late Dr. Alfred Clark in an investigation concerning the occurrence of prussic acid in maize and sorghum in relation to the human skin disease known as pellagra.

The record of his career clearly shows that he was a man of wide interests and sympathies. He continued to maintain a great interest in students from India for the remainder of his life, and his courtesy and kindliness will always be remembered by those few botanists who were privileged to know him during his time at Kew. When his death became known, the University College at Trivandrum was closed for a day in June 1954, as a token of the respect in which he was held.

C. R. Metcalfe.

Dr. **Herman Augustus Spoehr**, retired Chairman of the Carnegie Institution of Washington's Division of Plant Biology, Stanford, California, and Professor (by courtesy) in the Department of Chemistry at Stanford University, died on 21 June 1954, after a short illness. He was one of the first scientists in the United States to investigate seriously the process of photo-synthesis in plants. His book on *Photosynthesis*, published in 1926, is used by biologists and biochemists throughout the world. He was the author of *The Carbohydrate Economy of Cacti* (1919) ; *Studies in Plant Respiration and Photosynthesis*, with J. M. McGee (1923) ; *The Role of Research in the Development of Forestry in North America*, with I. W. Bailey (1929) ; *Fatty Acid Antibacterials from Plants*, with others of his staff (1949) ; and a large number of technical papers dealing with the chemistry of carbohydrates and plant physiology.

Dr. Spoehr was born in Chicago on 18 June 1885. He received his bachelor's degree from the University of Chicago in 1906. Thereafter he worked in the laboratories of Emil Fischer in Berlin and L. Maquenne in Paris, and returned to the University of Chicago to work with J. U. Nef. There he received his Ph.D. degree in 1909. He was appointed a staff member of the Carnegie Institution's Desert Laboratory at Tucson, Arizona in 1910. He and Mrs. Spoehr lived there until 1920 when they moved to the Institution's Coastal Laboratory at Carmel, California. In 1928, Dr. Spoehr became Chairman of the newly created Division (now Department) of Plant Biology, which was moved to the Stanford University campus in 1929. In 1930–31, he was Director of the Natural Sciences Division of the Rockefeller Foundation in New York, returning to Stanford in 1931 to resume the Chairmanship of the Division of Plant Biology. In 1950, he was called to Washington as a consultant to the Secretary of State. He was a member of the Executive Board of the Save-the-Redwoods League, and until a few years ago he served as Chairman of the Editorial Board of Annual Reviews, Inc. He was a member of the Board of Directors of the Forest Genetics Research Foundation, was on the Scientific Committee of the Board of Managers of the New York Botanical Garden, and was a Trustee of the California Section of the American Chemical Society.

Dr. Spoehr's scientific interests centered on the formation of organic matter by photosynthesis in plants. Contributory to this central interest, he made numerous investigations in pure carbohydrate chemistry, and in the occurrence and interconversion of carbohydrates in plants during the processes of plant respiration and photosynthesis. His achievement of bringing albino corn plants to maturity by artificial feeding derived from the central interest. He was also deeply concerned with the eventual application of basic research in photosynthesis to increasing the world's food supply. This concern led him to seek modification of the plant's composition by changing its environment—specifically to increase the protein and fat content of algae at the expense of the carbohydrates. This undertaking stimulated and contributed greatly to the recent rapid development of large-scale culture of algae for use as food. During the Second World War the laboratory that he headed concentrated on the study of antibiotics from photosynthetic organisms.

Dr. Spoehr's scientific eminence was recognized by election to membership in the American Philosophical Society, the American Academy of Arts and Sciences, Foreign Membership of The Linnean Society of London and honorary membership in the Deutsche Botanische Gesellschaft of Berlin. The University of Chicago conferred on him an honorary Doctor of Science degree in 1929 and gave him one of its Distinguished Alumni Awards in 1943. He was active in a number of learned societies and served as Vice-President of the American Society of Naturalists in 1946 ; President of the American Society of Plant Physiologists, 1944–45 ; and President of the Pacific Division of the American Association for the Advancement of Science, 1951–52. Dr. Spoehr was also a member of the Bohemian Club of San Francisco.

Though officially retired in 1950, Dr. Spoehr continued to be active in experimental work at the laboratory where he was always available to his scientific colleagues and friends for consultation and advice. He will also be remembered by many younger scientists for his constant inspiration and generous help.

He is survived by his widow, Florence Mann Spoehr, Palo Alto, California ; a son, Dr. Alexander Spoehr, an anthropologist and Director of the Bernice P. Bishop Museum, Honolulu ; a daughter, Mrs. Horace Miller, of Brooklyn, New York ; and a brother, Victor A. Spoehr, of Winnetka, Illinois.

James H. C. Smith.
C. S. French.

Professor **Felix Eugen Fritsch** was occupied with his numerous voluntary duties and his botanical work almost to the end, and although he was in poor health during the winter of 1953–54, it was not until mid-February that he became too ill to continue with his work. He died on 23 May 1954, at the age of 75.

Fritsch was born in Britain, of German parents, in 1879. He took a London first degree, which, he modestly claimed, was an ordinary pass degree and, without proceeding to honours, went abroad for the sake of his health, and studied at the University of Münich. On his return to England he spent some time at the Jodrell Laboratory, where D. H. Scott was then Keeper, and then accepted a temporary lectureship under F. W. Oliver at University College, London. This change was the beginning of an association with the University of London, which only ended with his death. In 1907 he became responsible for the teaching in the new Botany department at East London College. This appointment was a part-time one, for the department started in a very modest way and Fritsch records that when he went there the total equipment was six microscopes, a rocking microtome, an embedding oven and an oil-immersion lens. At first, classes were held only in the evenings, but in 1910, when day teaching started as well, Fritsch relinquished his assistant professorship at University College to devote the whole of his time to his work at East London College. Development of the new department, with limited resources, must have been uphill work and, apart from a demonstrator, Fritsch ran his department single-handed until E. J. Salisbury joined him as a full-time lecturer in 1912. Their association led to the appearance of several well-known and widely used botanical textbooks. Two of these, *An Introduction to the Study of Plants* and *An Introduction to the Structure and Reproduction of Plants* were later combined into *Plant Form and Function*, of which a new edition appeared in 1953. Fritsch retained his post, which was made a University Chair in 1924, until his retirement in 1948, when he was elected a Fellow of Queen Mary College. Simultaneously, the University conferred on him the title of Professor Emeritus.

Fritsch's activities in the University of London were by no means confined to his duties as head of a college department. He was an excellent committeeman and his services were much in demand at the University. He served on numerous University Committees and was, for a number of years, a member of the Senate.

College and University work did not claim the whole of his time. It was largely due to his initiative and zeal that the British Freshwater Biological Association was formed, and he was Chairman of its Executive Committee for twenty-three years. He was also anxious that algologists should have available a central collection of algal cultures and the one now housed at Cambridge owes its initiation largely to Fritsch. He was President of Section K of the British Association in 1927 ; became President of the Linnean Society at the age of 70 and, at 74, was still young enough to become President of the Institute of Biology. In 1953 he was elected President of the Association of Theoretical and Applied Limnology, an honour of which he was justly proud and one which afforded evidence of his intimate contacts with continental scientists. He was elected a Fellow of the Royal Society in 1932 and in 1950 was awarded its Darwin medal for his work on algae. In 1953 the University of London conferred upon him the degree of D.Litt. *honoris causa*. His last honour was the award of the Linnean medal, which was to have been presented to him at the Anniversary meeting of the Linnean Society: he died the day before. Fritsch's work was widely recognized abroad and he was elected an Honorary or Foreign member of a number of learned Societies, both in Europe and North America.

Fritsch's main interest in Botany throughout his life was the algae, of which his knowledge was vast and of world-wide repute. Early in his career he published two papers on plant anatomy in relation to systematics, but he will best be remembered by plant anatomists for his translation, in collaboration with L. A. Boodle, of Solereder's *Systematische Anatomie der Dicotyledonen* (1908). Although in his later years he claimed to know little about plant anatomy, and had, probably, not kept abreast of modern developments of the subject, his knowledge of formal plant anatomy was wide and exact.

As an algologist Fritsch was, at heart, a morphologist, although he showed, quite early in his career, a keen interest in algal ecology. His paper on *The role of algal growth in the colonisation of new ground and in the determination of scenery* was one of several based on his observations of algae during a visit to Ceylon. In 1913, jointly with Miss Rich, he published *A four years' observation of a freshwater pond* and in 1929 came the results of his investigations on *The encrusting algal communities of certain fast flowing streams*. In 1942, in collaboration with Miss John, soil algae came under review in *An ecological and taxonomic study of the Algae of British Soils*. He was also interested in the terrestrial algae and two papers on *The moisture relations of terrestrial algae*, one in collaboration with F. M. Haines, appeared in 1922 and 1923, preceded in 1916 by a detailed morphological and ecological study of the terrestrial *Zygogonium ericetorum*. On the morphological and systematic side he published numerous papers, including extensive surveys of African algae and of those of the South Orkneys and of Antarctica. One of his earliest papers, written in 1902 but not published until 1906 was a survey of the algae in *The Wild Fauna and Flora of the Royal Botanic Gardens, Kew*. Papers on individual algae included *Sphaeroplea* (1929), *Fischerellopsis* (1932) and *Cladophorella* (1944).

Fritsch's knowledge of the literature of the algae was immense. It is probable that in the future his bibliographical researches will be rated most highly, and tribute paid to his talents for interpretation and exposition. A comparison of the first edition of West's *British Freshwater Algae* (1904) with the second edition, which Fritsch revised and largely rewrote, twenty-three years later, will indicate how much the British algologist owes to Fritsch, both for his own work and for making Continental work widely known. His reviews of the algae also did much to bring knowledge of Continental work to Britain. Among such were his presidential address to Section K of the British Association (1927) on *Some aspects of present-day investigations of Protophyta*, his *Evolutionary sequence and affinities among Protophyta* (1929) and *Present-day classification of Algae* (1944). There was also his series of four papers, *Studies in the Comparative Morphology of the Algae* (1942–45), probably the most speculative he wrote, where his wide knowledge of the literature, and his deep interest in problems of phylogeny and taxonomy are well seen. On the ecological side, papers of this broader type include *Some aspects of the Ecology of Freshwater Algae* (1931), which formed the subject of his presidential address to the British Ecological Society, and *The Role of the terrestrial alga in Nature* (1936).

Fritsch's outstanding work was his two encyclopaedic volumes, *The Structure and Reproduction of the Algae* (1935, 1945), fitting memorials to his industry and scholarship, which are likely to remain standard reference books for the phycologist, especially on the morphological side, for many years. With their wealth of detail and illustration and their extremely comprehensive literature lists, of which it is said that every reference was checked by Fritsch personally, they are indispensable for any serious morphological work on algae. To the writer, not the least noteworthy feature of these two remarkable volumes is the terseness with which the possible affinities of the various groups are discussed. For one so interested in phylogeny, and with such an exact and detailed knowledge of algae, it must have been difficult to write with such commendable restraint on a favourite topic.

Of Fritsch as a man, others are more competent to write. He was fond of travel, loved his garden and was an accomplished violinist and ensemble player. He was among the kindliest of men, sincere, tactful, shrewd and sound of judgment; he was thorough in all that he did and satisfied only with perfection. He could have had few enemies—to know Fritsch was to like him.

F. W. JANE.

Dr. **Eugène Penard**, a Foreign Member of the Linnean Society of London, passed away in Geneva, Switzerland, on 5 January 1954, in the 99th year of a very full life. He was born in Geneva, on 16 September 1855, and there spent most of his years; indeed, his forebears had dwelt in the vicinity since the middle of the 14th century.

Dr. Penard was a man who combined precision with patience, extraordinary visual acuity with unusual artistic ability; above all, he was a modest person who possessed an insatiable intellectual curiosity, especially with regard to the wondrous world of microscopic life. Although his first scientific paper, his doctoral dissertation, did not appear until he had reached the age of 33, and at the age of 67 he was obliged to relinquish his cherished microscope because of danger to his eyesight, he became in the interim an internationally recognized authority on the protozoa. He published some 90 papers on the major groups of free-living fresh-water forms, flagellates, rhizopods, heliozoa, ciliates and suctoria; half a dozen of the principal works, now considered to be monographic classics in the field, alone total over 2000 pages in length. The exactness and accuracy of his microscopical observations are all the more remarkable when one is reminded that this naturalist from Geneva never owned an oil immersion objective. His eyesight probably could be ranked with that of Leeuwenhoek, the incredible Dutch microscopist of the 17th century, or with that of Dobell, the late renowned English protozoologist who was Leeuwenhoek's most distinguished biographer.

A man of many tongues, Penard thoroughly enjoyed travelling wherever fortune might carry him and he spent most of the years from 1881 to 1898 away from Geneva. He studied in Edinburgh and Heidelberg and did some work on the early development of the sea urchin at Naples, under Carl Vogt. He visited Algiers where he chanced to meet E. Maupas, the unobtrusive French librarian who was making such magnificent contributions to protozoology at that very time. Penard, then a youth of 29 years, engaged in animated conversation with the worthy gentleman totally unaware of his identity until years later. Penard also spent some months in the Rocky Mountains of America where he collected rhizopods and botanical specimens while living at the home of a close friend, Dr. John Gardiner, who was first head of the department of biology at the budding University of Colorado. A number of years away from home were spent in a tutorial capacity: first in Russia with the family of Prince Orloff, then in Germany in the home of Baron Belevski, and finally, for six years, again in Russia with Prince Youssoupoff. In the last-mentioned household he tutored young Felix Youssoupoff who later plotted the assassination of Rasputin. In Russia Penard was much too occupied with his duties even to remove his microscope from its case; he did succeed, however, in returning to Geneva (in 1898) with a wife.

Following Madame Penard's death in 1945, at the age of 89, Dr. Penard spent his last years in the Kermont Home on the outskirts of Geneva. It was there that I had the pleasure of spending a most delightful afternoon with him in the summer of 1952. Although his physical state did not allow him to go much beyond the confines of his little room, the mind of this nonagenarian remained sharp, his memory clear, his sense of humour enjoyable, and his voice as steady as his writing hand.

From the time of his first paper, which appeared in 1888, until his monograph on the ciliated protozoa in 1922, Penard published 78 papers, eight each in German and English, the rest in his native tongue, French. Except for his last short note (Habituation. *J. R. Micros. Soc.*, **67**, 43-45, with 3 figs.), the dozen works which came from his pen after 1922, generally observations of a more philosophical or psychological nature, were published in French. In addition to his treatises on the protozoa, Penard delighted in relating and writing tales of adventure for youngsters: five such works were published. Rich in the lore of natural history these books, to judge from their several reprintings, have been very popular with their youthful readers.

Recognition of his monumental contributions to the science of protozoology came to Penard at various times during his career. The Faculty of Sciences of Geneva twice honoured him with awards (in 1922 and 1945) and he was elected to membership in the leading biological and natural history societies of Geneva. He held the office of President of Honour of the Société suisse de Zoologie from 1936 until his death. Foreign or honorary memberships were bestowed upon him by the following scientific organizations: The Linnean Society of London (Penard was elected as a foreign member in 1911); The Royal Microscopical Society of London; the Queckett Club, London; Société française de microscopie; Société suisse de Microbiologie; the Society of Protozoologists (he became the first honorary member of this young society founded in America but international in membership).

By the death of Dr. Eugène Penard the scientific world has lost a lover of natural history beyond compare and a pioneer in the field of protozoology without peer. Fortunately his works will live on and the spirit of them may serve to inspire young biologically minded microscopists for some years to come.

JOHN O. CORLISS.

The Reverend **Arthur George Gregor** was born at Retford, Notts., on 25 May 1867 and died at West Worthing on 9 November 1954. Son of the Revd. G. Gregor he was educated at King Edward's Grammar School, Ashby de la Zouche, and later at Monmouth Grammar School. He received his theological training at St. John's College, Highbury, and University College, Durham, where he took his M.A. and later his B.D. His first curacy was close to the Wye Valley, but the rest of his life was spent in Sussex where he held curacies in the St. Leonards district, later became Vicar of Firle for nineteen years, and finally spent the last nine years of his life in retirement at Worthing. His intimate knowledge of the architecture of Sussex churches, and of Firle in particular, could hardly be rivalled.

A modest retiring soul whose true self was only known to very few, he was a life-long lover of flowers, and of the high places where some of the choicer species grow. His interest in botany began after he left school—in the country he was rarely seen without his vasculum, and Babington was his second Bible. He was in constant correspondence with leading botanists and Kew, and would never be satisfied until he had the exact identification of every plant that came into his hands.

He felt himself very deeply honoured when in 1948 he was elected a Fellow of The Linnean Society of London, partly on account of the extensive contributions he had been able to make to Wolley Dod's Flora of Sussex. He would have been equally delighted had he known that his large herbarium would eventually reach Kew. Rather surprisingly his membership of the Botanical Society of the British Isles only began in 1947 and continued until his death.

All his holidays were spent in the Swiss Alps and to the last his garden contained specimens of Silver Saxifrages collected by his own hands. There is hardly one of the well-worn pages of his Gremli that does not have its mouth-watering annotations of his findings with their appropriate dates. When circumstances denied him further trips to the mountains he loved so well he turned to the large garden of Firle Vicarage and amassed a splendid collection of trees, shrubs, herbaceous, alpine and rare native plants all of which he knew intimately and kept scrupulously labelled.

He was a very great student of the classics and literature and like so many of his generation had a phenomenal memory. He thought nothing of the fact that he could recite practically any given poem from the 'Golden Treasury' or thousands of lines from other sources, Latin, Greek or English, at a moment's notice. Once, to his great delight, he won a prize for the solution of a Greek crossword puzzle.

Needless to say he had a very keen ear for a false quantity in botanical nomenclature and woe betide the perpetrator of an unwitting discord such as Lĭlium or Gladiōlus ! One of the last additions to his very large and comprehensive library was a copy of Mr. H. Gilbert Carter's Glossary of the British Flora (now a prized possession of the writer's) which was discussed at great length at our last meeting and the markings in which recall so clearly his almost unfailing comment on any new fact which was brought to his notice, "Now what is the meaning of that ? ".

After thirty years' friendship the writing of these notes reveals only too clearly my own inadequacy for the task, but allows me not only to put on record my own appreciation of the enormous amount of knowledge gained from that long association, but also to ensure that one who perhaps did not receive his meed of recognition during his lifetime owing to his love of obscurity shall not go 'unhonoured and unsung'. KATHLEEN PICKARD-SMITH.

Henry Atkinson died, aged 82, on 24 December 1954.

He was an engineer by profession—a member of the Institution of Mechanical Engineers—but he never lost interest in the study of botany and biology, and after his retirement he spent ten years accumulating data for his book *Life Magnificent*, published in 1941 and better known in America than here.

Though unable to attend meetings of the Society in later years he still maintained a keen interest in all that concerned it and always appreciated the honour of being elected a member of the Linnean Society in 1907, when a young man, and as an expression of this he has bequeathed £100 to the Society.

SHELA M. ATKĪNSON.

Sir **John Stanhope Arkwright** (1872-1954), whose death took place in September 1954, was one of the leading personalities in the City and County of Hereford during the present century. The son of a distinguished father, who had been Lord Lieutenant and owner of the noble estate of Hampton Court, near Leominster, he entered Parliament at the age of 28 in 1900 as Conservative member for the Hereford Division, and retained his seat during the Liberal landslide of 1905 and at three subsequent elections during the Liberal administration. His ability, eloquence and popularity with both parties marked him out for office on a change of government ; but in March 1912 he was compelled by ill-health to resign his seat and some years later to retire from public life. But he had also earned distinction in two other directions, poetry and horticulture. At Oxford, in 1895, he won the Newdegate Prize with a poem entitled 'The Last Muster'. Twenty years later, his great hymn, 'The Supreme Sacrifice' was sung for the first time in Hereford Cathedral on the 4 August 1915, and thereafter at countless ceremonies of Remembrance throughout the Commonwealth and the United States. It may be doubted whether any hymn or poem, written in the present century, has touched more deeply the hearts of men and women throughout the English speaking world. His other absorbing interest was in his garden, and this ruling passion, for it was no less, remained with him from youth to old age. Keen sportsman though he was, he was always as happy with his daffodils as with his rod or his gun. In this, too, he won distinction. For many years he carried out experimental work which did a great deal towards improving the daffodil, and which entailed the sowing of an average of 4000 to 5000 seeds a year. He won a large number of successes at leading shows in the country, including the Single-heart Trophy at the Royal Horticultural Hall, London. In 1916 he caused much interest by producing a beautiful new flower, *Lychnis arkwrightii*—a cross between *Lychnis chalcedonica* and *L. haageana*—the merit of which was recognized by the award of the R.H.S. Botanical Certificate, 1912, the Standard Cup, Holland House Show, 1913, and the Silver Banksian Medal, Holland House Show, 1914. In 1934, Sir John accepted the Presidency of the Herefordshire Gardeners' Association. An expert hybridist, he lectured to the Association on more than one occasion. When the disabilities of old age and a long illness confined him to his house and garden at Kinsham Court, overlooking a deep wooded valley of the River Lugg on the Welsh Border, he still made his way whenever possible to the beds and greenhouses to pursue his research and experiments.

He was not ambitious of popular applause or public recognition although he achieved both; but the ambition to create or improve or develop, whether in poetry or horticulture or sport, was inherent in his character. As the heir to a great property and as a landowner in his own right he won the affectionate regard of all those connected with the two estates. He had made their interests and their sports his own, and he was manifestly repaid by their devotion. This was again apparent on the occasion of his marriage to the lady who was, with charm and grace, to share in his service to others no less than in the honours which he won. Though the bitter sorrow of a double bereavement and the shadow of ill-health clouded his later years, his major interest remained the welfare of his own people and of the county which he had served with such distinction. NIGEL DAVIDSON.

Dr. **Edward Stuart Russell**, O.B.E., who was our President from 1940 to 1942, died on 24 August 1954 at the age of 67. He will be remembered by the historians of zoology for his influence in three directions: in fishery science, in the study of animal behaviour and, especially, in the fundamental philosophy of our subject. His kind and sympathetic nature will never be forgotten by all those who have had the good fortune to be in any way associated with him. His power as an original thinker, revealed in his books, often came as a surprise to those from whom it had hitherto been hidden by his modesty and quiet manner. In this brief sketch of his life I will leave consideration of his philosophy to the end.

Edward Stuart Russell, the son of the Rev. John Naismith Russell, was born at Port Glasgow on 25 March 1887. From a primary school he won a bursary to Greenoch Academy and in 1904 went to Glasgow University. His interest in marine biology began at school as many old note books of this period show; and during University vacations he spent much of his time at the Millport Marine Station. At Glasgow, he studied zoology under Professor, now Sir John Graham Kerr and also saw much of Dr. J. F. Gemmill who introduced him to Professor, later Sir Arthur Thomson. When he had graduated, Russell became for a time Arthur Thomson's assistant at Aberdeen and they became great friends. He was not attracted to teaching and was wondering how he would make his living when he was offered a Carnegie Fellowship which he intended to take up at the Institut Oceanographique at Monaco. Just at this time, however, the Board of Agriculture and Fisheries, as it was then, had taken over the North Sea fishery investigations, which had been begun by the Marine Biological Association, and was advertizing for a zoologist to assist in dealing with the large amount of material collected. At Aberdeen, Russell had already examined some of the collections made by the Scottish research vessel *Goldseeker* and got interested in fishery work; instead of going to Monaco, he joined the Board of Agriculture and Fisheries in the spring of 1910. Thus began one side of his life's work.

In the following year, 1911, Russell started in his spare time to write *Form and Function*, the first of his philosophical studies, and so embarked upon another great line of activity which he kept up to the end. In this year too he married Jehanne Aurelie Minchin; it is from her that I have received much information about these early years before I knew him. She has told me how J. Arthur Thomson frequently came to London, where the fishery scientific staff then had their headquarters, so that they had many talks together on zoology and philosophy. They discussed the development of his *Form and Function* in all its stages, and Sir Arthur Thomson put him in touch with his great friend Professor Patrick Geddes. I shall return to this work of profound scholarship when I come to his philosophy ; it was published in 1916 after being finished under the difficult conditions of the war when he was out of London and out of touch with libraries.

In 1914, he wanted to join up with rest of his friends, but he was rejected on medical grounds. He threatened to resign from the Fishery Department unless he was given some work directly connected with the war ; so he was sent to the south coast to act as a liaison officer between the fishermen and the Admiralty. Mrs. Russell thinks these were some of the happiest days of his life. " His gift of getting on with people ", she writes," particularly at the extreme ends of the social scale, served him well and he made a great success of the job."

The Board of Agriculture and Fisheries had now been elevated to a Ministry and in 1921 Russell was appointed Director of Scientific Investigations. It was my good fortune in that year to be appointed Assistant Naturalist on his staff at the Fisheries Laboratory at Lowestoft. Russell did not try to tie the members of his staff to one set programme ; he encouraged each of us to develop research along the lines in which we were specially interested. In so doing he got the best out of his staff. Those days of the 'twenties were days of great production. Borley continued his former work on the plaice and Wollaston was working out his new mathematical treatment of plaice-egg distribution. Davis developed his quantitative studies of the bottom fauna and Savage similarly of the plankton. Graham investigated the stocks and biology of the cod and Hodgson of the herring. Lumby and Carruthers respectively did pioneer work in chemical and physical hydrology. I began an ecological study of the herring in relation to its animate environment. What thrilling and happy days they were. In describing Russell's influence I cannot do better than quote from another obituary by Michael Graham :

> " All that a man on his staff needed was the knowledge that the Director would drop in every few weeks, and in a very few minutes understand fully what progress had been made, and immediately illuminate the next ground to be trodden. He rarely suggested that one was under any obligation to take his advice, but one usually did."

Russell himself added much to the natural history of the cod and haddock by two large reports he made analysing the copious statistical data collected regarding the quantities and sizes of fish landed at the various ports before the first world war. As a result of this work he introduced the division of the North Sea into a large number of rectangles for the collection and plotting of the trawl-fishery statistics from 1920 onwards. In each rectangle, for every month of the year, year after year, the average weight of fish per hundred hours fishing are recorded for the more important species of fish ; such data, obtained from trawler skippers by collectors at the ports and plotted on monthly charts, have given much information on the fluctuations of the fisheries over the years. Perhaps Russell's greatest contribution to fisheries science was his simplification of the overfishing problem by his paper published in 1931 in which he swept away so much confusion of thought on the matter by expressing in a simple algebraic equation the different factors concerned :

$$S_2=S_1+(A+G)-(C+M)$$

where S_1 and S_2 respectively represent the weight of catchable stock (i.e. those fish over a certain size) at the beginning and at the end of a year. A represents the addition during the year of catchable fish from noncatchable stock (i.e. young recruits coming to be of catchable size) and G is the added weight by growth of both S_1 and A ; C is the weight of fish caught during the year and M that of fish dying by natural mortality. He then showed how the yield in fisheries could vary according to the different values of A, G and C, there being little change in M. Rational exploitation means a stabilized fishery with $S_2 = S_1$, which means $A+G$ must $= C+M$. These latter may, however, be equal at different levels : if C is low $A+G$ will be low because food is limited—and the fishery will not be yielding its maximum output. We can increase C up to a point, the point of most economical fishing, beyond which overfishing occurs. Before the appearance of this simple statement there had been endless discussion and misunderstanding through different people looking at the problem from separate viewpoints and stressing one or other side of the question without seeing it as a whole. Russell's paper was a landmark which led on to the more exact and mathematical treatments of Graham, Beverton and Holt. In 1939 he was invited to give the De Lamar Lectures at the Johns Hopkins University and he took overfishing as his subject ; they were subsequently published in 1942 as *The Overfishing Problem* (Cambridge University Press), a most lucid account of all the factors concerned, with excellent examples taken from actual fisheries.

Russell was a prominent member of the International Council for the Exploration of the Sea and editor of its new *Journal du Conseil* from its beginning in 1926 to its temporary stoppage through the war in 1939 ; he was also for a time Chairman of the Consultative Committee. He greatly enjoyed the annual meetings with his continental friends and through this friendship had an important influence. From 1930 to 1935, with the help of his colleague Mr. F. M. Davis, he successfully led the campaign to persuade the European governments to enforce a regulation determining the minimum size of mesh for nets and of fish allowed to be marketed ; this was a very important step forward in international agreement.

Until 1945 Russell held the Directorship of Fishery Investigations and was then Fisheries Scientific Advisor for two years after his retirement. Alongside this stream of fishery activity which involved a great deal of administration, he kept up his work on the more philosophical side of zoology ; that was his main interest—his real passion in life. It lead him to his third but related line of study, that of animal behaviour ; in spite of his busy civil service life he was able, since he was much at the Ministry headquarters, to be Honorary Lecturer in Animal Behaviour at University College, London, from 1932 to 1947. This, however, was a consequence of his philosophical approach ; so let us return to that. As early as 1909 he began contributing a number of articles to *Scientia* on theoretical zoology ; their titles give their scope : ' Some hypotheses on the structure of the germ plasm ' (1909), ' The Evidence for Natural Selection ' (1909), 'Evolution ou Epigénèse' (1910), 'Vitalism' (1911), 'Le Problème des Espèces et de leur Origine ' (1915). These were thrown off in the preparation of his *Form and Function* (1916) which has the subtitle of *A Contribution to the History of Animal Morphology*. It is nearly forty years since it was published, but it is as readable and as important today as it was then; I am sure there are many who will agree with me that it is a zoological classic. As some of the younger generation may not know it, I will give an indication of its theme by quoting Russell's own words from his preface :

> " This book is not intended to be a full or detailed history of animal morphology . . . My aim has been rather to call attention to the existence of diverse typical attitudes to the problems of form, and to trace the interplay of the theories that have arisen out of them.
>
> " The main currents of morphological thought are to my mind three—the functional or synthetic, the formal or transcendental, and the materialistic or disintegrative.
>
> " The first is associated with the great names of Aristotle, Cuvier, and von Baer, and leads easily to the more open vitalism of Lamarck and Samuel Butler. The typical representative of the second attitude is

> E. Geoffroy St. Hilaire, and this habit of thought has greatly influenced the development of evolutionary morphology.
>
> " The main battle-ground of these two opposing tendencies is the problem of the relation of function to form. Is function the mechanical result of form, or is form merely the manifestation of function or activity ? What is the essence of life—organization or activity ?
>
> " The materialistic attitude is not distinctively biological, but is common to practically all fields of thought. It dates back to the Greek atomists, and the triumphs of mechanical science in the 19th century has induced many to accept materialism as the only possible scientific method. In biology it is more akin to the formal than to the functional attitude."

The book is a most scholarly and illuminating account of the interplay of these three main currents of morphological thought from the days of Greek speculation to the end of the last century. No matter what our viewpoint may be, it is a valuable and stimulating history. His own views are clearly brought out in the last few sentences of the book :

> " Dogmatic materialism and dogmatic theories of evolution have in the past tended to blind us to the complexity and mysteriousness of vital phenomena. We need to look at living things with new eyes and a truer sympathy. We shall then see them as active, living passionate beings like ourselves, and we shall seek in our morphology to interpret as far as may be their form in terms of their activity.
>
> " That is what Aristotle tried to do, and a succession of master-minds after him. We shall do well to get all the help from them we can."

His next book *The Study of Living Things* (1924) was a much smaller book ; it had the subtitle of *Prolongomena to a Functional Biology*. This was not history, in it he was feeling his way towards his philosophy of the organism. I do not think it was an easy book to grasp. At a first reading, I remember feeling disappointed that there was not more in it, yet I felt I was not getting it all ; it was only at the second reading that I began to realize that it was more profound than I had thought. He put forward what he calls the psycho-biological or the functional view and asked us to " look upon living things with an unprejudiced eye, recording their activities as we see them, without seeking to destroy, by analysis, their unity, co-ordination and intention". He began here to develop his conception of what he later calls directiveness :

> " The essential difference between the inorganic unit and the living individual is that the activities of all living things tend towards some end and are not easily diverted from achieving this end. Let no one say that this is a fanciful reading of the facts. It is impossible for anyone, whatever his philosophical prejudice may be, to deny that all goes on in the organic world *as if* living beings strove actively towards an end, whether of self-development, self-maintenance or the continuance of the race. And if we interrogate our own deepest experience we find, as the ultimate driving force of our life, deep-seated conative tendencies or instincts, of which we may normally be totally unconscious, but which impel us to courses of action which we may or may not be able to rationalize.
>
> " We may conclude then that what differentiates a living thing from all inorganic objects or units is this persistence of striving, this effort towards the expression of deep-lying tendencies, which we know to be the inmost core of our own being."

His next work was a larger one, on the lines of his *Form and Function*, but dealing with the various theories of development : *The Interpretation of Development and Heredity* (1930). Here he regarded heredity as essentially a problem of development and again stressed the conception of directiveness.

"The developing organism," he writes, "acts *as if* it were fulfilling an end or purpose—that of arriving at the typical form and modes of activity of the species ; it tends towards this goal in spite of difficulties and the end is more constant than the way of attaining it". Here again, he made a splendid historical and comparative review of the various theories bearing on the problem, but it is clear that he was not in sympathy with the theory of the gene and some may feel he hardly did it justice.

In 1934, he was President of Section D of the British Association at its Aberdeen meeting and made 'The Study of Behaviour' the subject of his address ; in this he stressed again what he has called the organismal point of view. In the same year he published his excellent book on *The Behaviour of Animals* which was an expansion of his course of lectures at University College London ; it went into a second edition in 1938 and was a great stimulus to a more direct study of the living animal under natural conditions. His three Presidential Addresses to our Society, in 1940, 1941 and 1942, dealt with different aspects of instinctive behaviour and in them he collected a large number of illuminating examples which will always be a mine of reference for the student.

In 1945, Russell published his striking little book *The Directiveness of Organic Activities*. In this he brought together a number of very remarkable instances of this directive activity which he regards as a characteristic of life. He did not regard it as purposive, because the organism, even if it were conscious, could not usually be aware of the goal towards which its activity is directed. Particularly interesting are the cases in which the activity may be variable ; if the goal is not reached by one method then others may be employed, or if a combination of methods is normally used, deficiency of one may be compensated for by an increased use of another. He presented no main theory to explain the phenomena ; he was content to point out the extent of this directiveness in nature and to urge its importance in the understanding of the organism. In this he has done great service as a pioneer. Others will follow in an attempt to analyse this directiveness into other components, whether they will succeed only time will show.

There can be no doubt that to Russell this directiveness appeared as an *irreducible* characteristic of life. He ends his essay on this subject with a chapter on the concept of organism and I cannot do better than end this brief article by quoting his final paragraph which so clearly expresses his philosophical and biological outlook :

> " Our conclusion that life processes are essentially and fundamentally directive and creative may be rejected as 'metaphysical' or 'mystical'. It is of course nothing of the sort. I make no hypothesis as to the philosophical basis or 'ground' of directiveness and creativeness. I merely accept the patent evidence that they are characteristic of living things and of them alone. Nor do I suggest anything strange in the way of method. I suggest simply that, instead of making continual and vain efforts to squeeze biological facts within the materialistic frame, and attempting analysis without end, we accept them as *biological*, that we deal with the problems of development, maintenance and reproduction in terms of observable activities of the organic agents concerned without making the gratuitous hypothesis that these activities are mechanistic. Only in this way can we hope to establish the laws of organic activity."

A. C. HARDY.

SOME OBSERVATIONS ON DACTYLORCHIS INCARNATA (L.) VERMLN. IN THE BRITISH ISLES

By J. Heslop-Harrison.

(With Plate 1 and 13 text-figures.)

Introduction.

In Vermeulen's classification of the genus *Dactylorchis* (1947), the early marsh orchid, *Dactylorchis incarnata* (=*Orchis incarnata* auct. mult., *O. strictifolia* Opiz, *O. latifolia* L. sec. Pugsl.) is placed in the section *Incarnatae* Vermln. with *D. cruenta* (Müll.) Vermln. and *D. salina* (Turcz.) Vermln. The discrimination of *D. cruenta* and *D. salina* as taxonomic species rests upon a somewhat slender basis: von Soó (1930–40, p. 212) treats *Orchis salina* Turcz. as equivalent to a subspecies of *O. incarnata*, while Vermeulen (1947, p. 124) has himself suggested that *O. cruenta*, previously placed as a subspecies under *O. incarnata* by Ascherson & Graebner (1907), is perhaps best kept in that rank under *Dactylorchis incarnata*.

Being delimited by a number of rather clear qualitative diagnostics, the subsection as a whole is quite distinct within the genus, and all of the plants referable to it which have so far been investigated cytologically have a chromosome number $2n=40$, which is the basic diploid number of the genus. From the other two British subsections of the Section *Maculatae* of *Dactylorchis*, the *Incarnatae* may be keyed out as follows (Heslop-Harrison, 1954 a & b):

1. Stem solid throughout most of its length; upper non-sheathing bract-like leaves two or more in number; lower bracts relatively narrow (<3 mm.); flower spur slender (<2 mm.); chromosome numbers $2n=40$ and $2n=80$ .... *Eumaculatae*

   Stem usually hollow throughout most of its length; 0, 1 or 2 non-sheathing, bract-like leaves on the upper part of the stem; lower bracts relatively wide (>3 mm.); spur usually stout (>2 mm.) 2

2. Stem cavity wide (usually exceeding ½ total diameter); leaves yellow-green, usually erect or only slightly recurved, narrowing almost from the base; leaf tip markedly hooded (cucullate); flowers relatively small, labellum generally less than 8 mm. in width (larger in subsp. *gemmana*), its sides often more or less strongly reflexed laterally; chromosome number $2n=40$ .... *Incarnatae*

   Stem cavity medium or small, leaves dark green, often spreading, broadest about one third of their length from the base, ovate (linear in *D. traunsteineri*), apex not or only slightly hooded; flowers mostly large (smaller in *D. purpurella*), labellum generally considerably greater than 8 mm. in width, its sides more or less reflexed laterally (*D. majalis*, *D. traunsteineri*, etc.) or not at all (*D. purpurella*, *D. praetermissa*); chromosome number $2n=80$ .... *Majales*

Within the limits of the subsection *Incarnatae* there is a remarkable amount of morphological variation, as may be judged from any of the recent descriptions of the species *D. incarnata* itself (e.g. Summerhayes, 1951, and Clapham, 1952), and from former more or less elaborate attempts at its taxonomic subdivision (Ascherson & Graebner, 1907; E. G. & A. Camus, 1928–29; Pugsley, 1935; von Soó, 1930–40; Vermeulen, 1949). In spite of the striking polymorphy of the species, however, no really satisfactory taxonomic subdivision has in fact proved possible, and it seems probable that none ever will be entirely satisfactory which depends upon the recognition of 'types'. *D. incarnata* reveals a mixture of continuous and discontinuous variability, and although it is possible to select certain forms characterized by distinctive assemblages of characters as a basis for the establishment of infraspecific taxa, it is not possible to treat all of the variation in this manner, since the systems of correlation upon which such treatment depends all break down in some parts of the range of the species. The variation is, in fact, *reticulate*, in the sense of Turrill (1950).

Vermeulen (1949) has attempted to approach the problem by describing and naming large numbers of paramorphs—no less than nineteen from Holland alone—characterized by single character differences. Were it possible to distinguish all biotypes in this manner, then no doubt any population could be described in terms of its biotype composition. But the method is, of course, taxonomically clumsy, and takes no account at all of the genetical unity of breeding populations.

Pugsley's treatment (1935) of the infraspecific variation of *D. incarnata* in the British Isles pays some attention to ecological and distributional factors, but it also is essentially typological. As the type form of the species, he accepted that with pale salmon-pink or flesh-coloured flowers, and in addition he recognized five varieties, for which the following names and brief descriptions were provided under the species name adopted by him, *Orchis latifolia* :

> var. *gemmana* Pugsl. Plant tall, up to 1 m. in height ; leaves usually very long, spike long, many-flowered, nearly all the bracts longer than the flowers.
>
> var. *ochroleuca* (Boll) Pugsl. Plant tall, up to 50 cm. ; flowers straw-coloured with yellowish lip. (In his paper of 1935 Pugsley did not accept this as British ; later (1939) he reported it as occurring in East Anglia.)
>
> var. *pulchella* (Druce) Pugsl. Flowers larger than in the type, bright reddish purple, with sub-entire lip, 8 mm. long and 7–8 mm. broad, strongly variegated with darker lines and but little laterally reflexed.
>
> var. *coccinea* Pugsl. Plant usually rather dwarf, with upper leaves sometimes exceeding the spike. Flowers bright, clear crimson-red (becoming maroon in dried specimens) with lip less well marked and less laterally reflexed than in the type.
>
> var. *cambrica* Pugsl. Plant rather dwarf, up to 20 cm. high. Flowers purple, with short (5–6 mm. long and broad) scarcely lobed lip subequalling the blunt, faintly spotted lateral sepals. Spur short, thick, about half as long as the ovary.

Additional information given by Pugsley (1935, 1939) in reference to synonymy, illustrations, herbarium material and to the British stations for the plants upon which some of the varieties were based, makes possible the adoption of most of these names, at least for the purpose of initial reference, in a sense similar to the original. Those which can be so used have been accepted as a basis of reference in this paper, the varieties being raised to the rank of subspecies under *Dactylorchis incarnata*. The modified nomenclature is as follows (Heslop-Harrison, 1954 a & b) :

subsp. *incarnata* (*D. incarnata* subsp. *lanceata* (Dietr.) Vermln.).
subsp. *coccinea* (Pugsl.) H.-Harr.
subsp. *gemmana* (Pugsl.) H.-Harr. f.
subsp. *ochroleuca* (Boll) H.-Harr. f.
subsp. *cruenta* (Müll.) Vermln.
subsp. *pulchella* (Pugsl.) H.-Harr. f. (including *Orchis latifolia* var. *cambrica* Pugsl.).

The main departure from Pugsley's treatment is in the addition of *O. cruenta* as a subspecies, and in the grouping of all other populations with predominantly magenta-purple flower colour, including Pugsley's var. *cambrica*, under subsp. *pulchella*.

As applied in this paper, these subspecies may be keyed out as follows :

1. Anthocyanin pigmentation totally absent from the plant ; flowers creamy, or yellowish white ; labellum mostly shape grade 1 (fig. 2)	subsp. *ochroleuca*
Anthocyanin pigment present in the flowers ; labellum shapes mainly grades 2, 3, 4 and 5	2
2. Flower colour flesh- or salmon-pink	3
Flower colour purple, magenta, ruby- or crimson-red, to maroon on drying	4
3. Labellum small (<8 mm. in width, <7 mm. in length), pattern mostly grade 3 (fig. 1) ; leaves usually four or five in number ; overall stature up to 40 cm.	subsp. *incarnata*
Labellum large (>9 mm. in width, >7 mm. in length), pattern mostly grades 1 and 2 ; leaves six or more in number ; stature often greatly exceeding 40 cm.	subsp. *gemmana*
4. Flower colour magenta or purple, with no trace of brick-red or maroon, labellum shape mostly grades 4 and 5	5
Flower colour ruby- or brick-red to maroon ; labellum shape mostly grades 2 and 3 ; leaves often relatively broad and recurved	subsp. *coccinea*
5. Leaves without spots, blotches or fields of colour	subsp. *pulchella*
Leaves of some individuals with spots, blotches or zones of reddish or purplish pigment, mostly on both upper and lower surfaces	subsp. *cruenta*

While this treatment is probably the most expedient from the point of view of orthodox taxonomy, it constitutes no more than a formalized representation of the variation pattern of *D. incarnata*. It will be apparent from the more detailed analysis of the structure of the species in the British Isles which follows that the ‘ subspecies ’ cover, in effect, habitat races which, while all intergrading to some extent, nevertheless show some degree of morphological differentiation. In addition, however, there exist other populations which cannot justifiably be included anywhere in this scheme of classification, and limitations must therefore be placed upon the application of the names in practice.

THE SCOPE OF FLOWER VARIATION IN *D. INCARNATA*.

(*a*) *Colour.*

The range of flower colour encountered in *D. incarnata* transcends that in the whole of the remainder of the genus. The specific epithet refers to the flower colour characteristic of the subsp. *incarnata*, usually described as flesh- or salmon-pink. Approximate matches to the tones found in this form are given by Séguy tints 18, 19 and 20 (Séguy Colour Standards, 1936). The illustration given by Fischer & Nelson (1931) for *Orchis incarnata* provides a good representation. The plate provided by Clarke (1882), one of the earliest botanists to describe and illustrate what is undoubtedly a form of *D. incarnata* from Britain, exaggerates a feature seen in some individuals referable to subsp. *incarnata*, namely a tendency for the central area of the labellum to assume a straw-coloured or yellowish tinge. The extreme variation in this direction is seen in subsp. *ochroleuca*, in which the concolorous flowers are yellowish white or cream-coloured, and entirely without any pinkish or reddish tinge. A greenish hue is, however, occasionally present, particularly in the labellum near the spur mouth, and an approximate match to the tone is given by the Séguy tint 270.

There is often a considerable variation in intensity of flower colour in populations referable to subsp. *incarnata*, and data concerning this in some Hebridean populations, obtained with a simple comparison colorimeter, have been published elsewhere (Heslop-Harrison, 1948). In the arbitrarily scaled colorimeter employed in these tests, the modal class for subsp. *incarnata* was grade 9, roughly corresponding with Séguy 19, and this seems to be general throughout the British Isles. Small numbers of individuals in the Hebridean populations have more intense flower colours, ranging up to grade 3 of the colorimeter employed, near Séguy 31. In populations referable to subsp.

coccinea because of prevailing flower colour, the modal labellum colour class corresponds to grades 4 or 5 of the colorimeter used in the Hebridean investigation, i.e. somewhat more intense than Séguy 51, a colour described by Pugsley as crimson-red. A moderately good representation of the shade, necessarily duller than in life, is given in the Stephensons' Plate 556, fig. 4 (1920). The deep colour of subsp. *coccinea* seems to represent simply an intensification of the shade encountered in subsp. *incarnata*.

In contrast, the flower colour dominating in populations placed under subspp. *pulchella* and *cruenta* is qualitatively different, being essentially purple-magenta. An approximate match to it is provided by Séguy tints 58 and 59, although these do little justice to the intensity and clarity of the hue, surpassed only by that of *D. purpurella* in the British dactylorchids.

The pigments responsible for the flower colorations of the dactylorchids are formed in the sap of the epidermal cells of the tepals. The main anthocyanin present appears to be a cyanidin ; in some colour forms this is probably coupled with an anthoxanthin co-pigment. A possible scheme of flower colour interrelationships is as follows :

Cyanidin (co-pigment absent or phenotypically insignificant)	——	subsp. *pulchella* subsp. *cruenta*
Cyanidin with anthoxanthin co-pigment	dilute	subsp. *incarnata* subsp. *gemmana*
	intense	subsp. *coccinea*
Anthoxanthin (no anthocyanin present)	——	subsp. *ochroleuca*

In some colonies otherwise referable to subsp. *pulchella* anthocyanin-less individuals are present in small numbers ; as would be expected from a system like the above, these are dead white and not ochroleucous, i.e. true albinos for flower colour. This fact is commented upon by T. & T. A. Stephenson (1923), Nannfeldt (1944) and Summerhayes (1951). In colonies of subsp. *incarnata* in East Anglia, similar anthocyanin-less individuals occur ; these partial albinos match subsp. *ochroleuca* in colour (again as would be expected from the above scheme) and indeed would be indistinguishable from individuals of typical *ochroleuca* populations were it not for differences in labellum shape.

(*b*) *Flower patterning.*

The labellum patterning most commonly found in the subsp. *incarnata* is in the form of a pair of angular loops of purplish or reddish pigment, narrowed towards the mouth of the spur, enclosing an irregular pattern of dots and short bars (fig. 1, 3). In the absence of circumscribing loops, the labellum may show irregular flecking or dotting, generally concentrated towards the opening of the spur (fig. 1, 2 ; cf. Vermeulen's var. *noncircumscripta*, 1949). A sequence of intermediates connects this with the totally unpatterned, concolorous type. Intensification of labellum pattern is usually accompanied by the disruption of the pattern into heavy irregular bars or spots (fig. 1, 4).

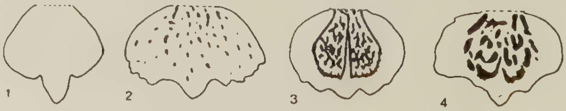

FIG. 1.—Labellum patterns in *D. incarnata*.

The sequence of patterns shown in fig. 1 appears to be logical, even though no developmental relationship may exist. The four types illustrated have been selected as standards for the assessment of flower patterning in some of the populations discussed below.

(c) *Labellum shape.*

In the fresh state the very characteristic appearance of the flowers of the *Incarnatae* is due to the reflexion of the lateral lobes of the labellum. This may be so extreme that these lobes come into contact, when the flower as a whole presents a remarkably strict appearance. During the life of the individual flower there is a gradual change in this character, since the labellum, as in other dactylorchids, is involute in the bud. The maximum reflexion is usually attained two or three days after opening. After pollination, turgidity is lost and the rigid reflexed posture with it.

This reflexion of the lateral lobes obscures to some extent the very considerable variation in labellum shape and size in the *Incarnatae*, variation which is only apparent when the labellum is flattened. Apart from variation in proportion of length to width, in those forms in which the labellum is three-lobed, the sinus depth and width varies within wide limits. Although variation of this complicated form does not readily lend itself to biometrical assessment, a resort to scoring methods is possible, as with labellum patterning. For this purpose, the five shapes illustrated in fig. 2 have been adopted as standards which represent more or less equally spaced points in the shape variation range.

Labellum size, where recorded below, has been measured as maximum width, and length from the mouth of the spur to the tip of the central lobe.

(d) *Spur size.*

Where recorded below for population samples, spur size refers to length from mouth to tip, and width about 1 mm. from the mouth where flattened ; the latter figure represents thus not the diameter, but approximately half the circumference at this point.

Floral Variation and Environmental Influence.

The stability of floral characteristics in cultivation after transplanting from the wild has been examined in plants from populations conforming with subspp. *incarnata*, *pulchella*, *coccinea* and *ochroleuca*. Individuals of subspp. *pulchella* and *coccinea* have been maintained in active growing state in pot cultivation for three successive seasons with normal yearly flowering, but it has not yet proved possible to establish the conditions in which subspp. *incarnata* and *ochroleuca* will flower for more than the first season after transplanting. These plants mostly show a continuous decline in vigour after transplanting, and generally produce a barren rosette in the second year in cultivation, usually succumbing altogether in the third. This is possibly attributable to their need for an active movement of well-aerated, base-rich water in the rooting layer.

Notwithstanding the difficulties of cultivation, sufficient evidence has already been obtained to confirm the expectation that the characteristic flower hues and patterns of the various subspecies are not influenced to any detectable extent by cultivation conditions. Pigment intensity, can, however be modified in the normally more deeply coloured forms, since it is dependent upon the insolation during the period of flower opening. The degree of control is illustrated by an experiment on a sample of plants from the very uniform population of Walton Common (the characteristics of which are discussed under P3 below) brought in from nature on 1 June 1953, and allowed to open flowers (*a*) in full daylight, (*b*) in semi-shade (*c*. 40 per cent daylight), and (*c*) moderately deep shade (5-10 per cent daylight). The effects are recorded in Table I.

TABLE I.—Labellum pigmentation in differing intensities of illumination. (Pairs of plants from colony P3, Walton Common.)

Illumination	Colour	Pattern
100 % daylight	Séguy 58 (deep magenta)	Normal (fig. 1, grade 3)
40 % daylight	Séguy 4 (rose pink)	Faint, but normal in form
5–10 % daylight	Séguy 5 (very faint pink)	Only apparent near spur mouth

Transplantation has had no detectable effect on the range of labellum shape in any of the individuals of the four subspecies studied ; that is to say, no differences have appeared of a magnitude sufficient to move an individual from one grade to another of fig. 2. Labellum and spur size is likewise not appreciably influenced in those plants which succeed in cultivation. In languishing plants of subsp. *incarnata*, abnormal flowers do appear with reduced labella, but this fact can have little significance in relation to the variation of healthy colonies in the wild.

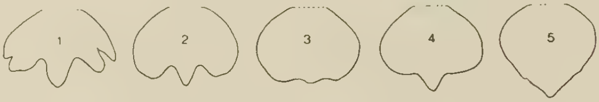

FIG. 2.—Labellum shapes in *D. incarnata*.

These are merely preliminary observations on transplantation experiments carried out during 1948–1950, and recommenced in 1953. Fuller results, including those concerning the somewhat more plastic vegetative features, will be reported elsewhere.

VARIATION AND CHARACTER CORRELATION IN SOME BRITISH POPULATIONS.

A distinction may be made between the discontinuous form of variation, seen in flower colour and to some extent in flower patterning, and the continuous type, apparent in metrical features and in such attributes as pigmentation intensity. Presumably the qualitative differences in tepal pigment are oligogenically controlled whilst the quantitative variation in the various metrical characters has a polygenic basis. The subspecies established above are based upon criteria of both forms, but two of the effective subdivisions depend essentially upon qualitative differences in flower colour, reinforced by certain less positive quantitative morphological differences. As already indicated, this type of correlation is not by any means universal, and it is its breakdown which prevents the extension of the taxonomic subdivision given above to all populations of the species.

This point, and also the ecological aspects of the variation, are best illustrated by an actual analysis of some typical populations. Those discussed below exemplify a number of different situations. In those classed as ‘ monomorphic ’, the variation of morphological features is continuous, and distinct, non-intergrading classes of individuals cannot be recognized within them. All but the most variable can be satisfactorily grouped under subspecific names as these have been defined above. In the populations termed ‘ polymorphic ’, the individuals fall into two or more well-marked classes, mostly on a basis of flower colour.

The locations of the populations described below are indicated in fig. 3. Among them, they span practically the entire ecological range of *D. incarnata* in the British Isles. Uniformity of habitat has been a primary consideration in the selection of most of them, with the two-fold aim of clarifying ecological

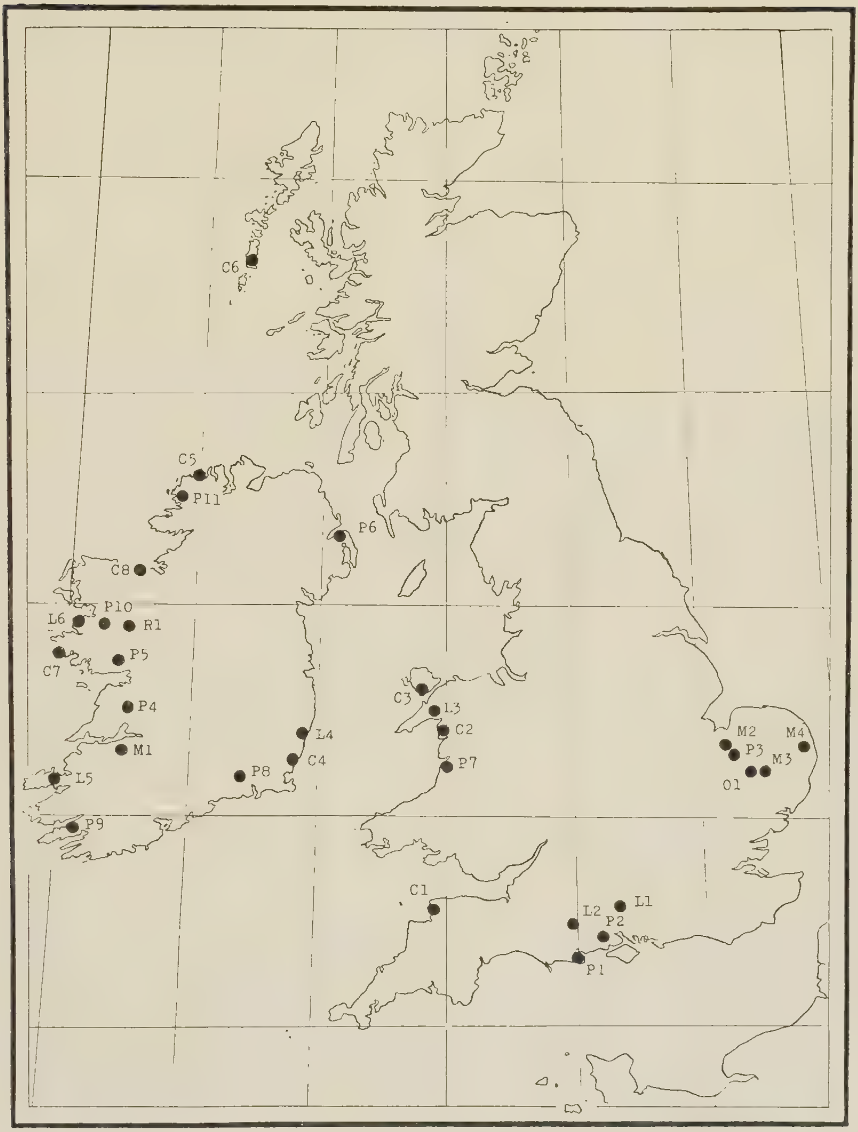

FIG. 3.—Location of the populations mentioned in the text.

relationships and also of eliminating to some extent intra-population variability due to the direct influence of local environment. Habitat uniformity has been judged principally from the homogeneity of the plant associations of the sample sites ; where, in any particular locality, diverse communities are intermingled plants have been collected, wherever possible, consistently from the same community-type.

Occasionally the limits of the sampling area have coincided with what are the probable effective limits of the gamodeme ; that is to say, for a considerable distance beyond the boundaries of the selected communities in these instances dactylorchids are sufficiently infrequent to make it unlikely that a high level of gene flow prevails, either inwards or outwards. Mostly, however, there is no such guarantee ; what has been sampled is a segment from an ecologically homogeneous area of a large and relatively diffuse breeding unit, itself extending, with varying densities of individuals, over a mosaic of slightly varying habitats.

MONOMORPHIC.

Subspp. *incarnata* and *coccinea*.

The following six populations referable to subsp. *incarnata* fall roughly into three groups according to the nature of their habitats, viz., (*a*) water meadows adjoining rivers on the chalk, (*b*) topographical marsh, and (*c*) dune marsh.

L1. Water meadow west of the river Itchen, near Otterbourne, Hampshire.
L2. Water meadow, on an island in the river Test, near Longstock, Hampshire.

The vegetation of these water meadows varies considerably according to height above water table, drier stretches, with dominance of *Dactylis glomerata*, *Cynosurus cristatus*, *Festuca rubra*, *Holcus lanatus*, *Anthoxanthum odoratum* and other grasses, alternating with wetter regions in which rush and sedge vegetation prevails. The marsh orchids, in both localities *D. incarnata* and *D. praetermissa*, are mostly restricted to areas of waterlogged mineral soil. The samples of *D. incarnata* were collected from colonies growing in association with *Carex acutiformis*, *C. disticha*, *C. panicea*, *C. nigra*, *C. glauca* and some *C. rostrata*, with the bottom moss *Acrocladium cuspidatum*. The pH of the surface water in each locality was 7·0–7·2.

L3. Margin of valley bog, near Pentglass, Caernarvonshire.
L4. Coastal marsh south of Newcastle, Co. Wicklow.

In the first of these localities, the orchids occur in marginal sedge meadow in a region of heavy silting. Here *Carex lasiocarpa* is dominant, with *C. rostrata*, *C. panicea*, *C. lepidocarpa*, *C. glauca* and *C. nigra*. *Equisetum limosum* and *Thelypteris palustris* are locally important components of the vegetation, with the mosses *Acrocladium cuspidatum*, *Campylium stellatum* and *Drepanoclados revolvens*. The soil-pH here is *c*.6·2 ; towards the centre of the bog it drops to 5·0, and *D. incarnata* does not occur in this area, where *Juncus sylvaticus*, *Molinia caerulea* and *Eriophorum angustifolium* dominate with *Sphagnum palustre* and *S. papillosum*.

In the second locality, *D. incarnata* occurs mainly in the patches of sedge meadow which are scattered throughout the extensive area of *Phragmites*- and *Cladium*-dominated fen lying on the landward side of the railway track which runs along several miles of the shingle beach on this part of the Wicklow coast. The sample was taken from such an area, where associated species were *Carex acutiformis*, *C. lepidocarpa*, *C. rostrata*, *C. disticha*, *C. nigra* and *C. glauca* with some *Phragmites*, *Juncus subnodulosus and Schoenus nigricans*. The soil in the sample area is a mineral-rich peat with a pH *c*. 7·0.

L5. Marsh at the south end of Lough Gill, Castlegregory, Co. Kerry.
L6. Marsh at Dooaghtry, Co. Mayo.

These two habitats are essentially similar : dune marshes, in which the soil contains a high percentage of calcareous sand, the pH in each case lying between 6·5 and 7·0. In each locality, sedges form the dominant vegetation, mainly *Carex rostrata*, *C. glauca*, *C. nigra*, and *C. panicea* ; *Phragmites*, *Equisetum palustre*, *Eleocharis palustris* and *Juncus sylvaticus* are also present in both, and *Schoenus nigricans* in the marsh near Lough Gill. Characteristic dicotyledons include *Menyanthes trifoliata*, *Samolus valerandi*, *Ranunculus flammula*, *Caltha palustris*, *Lychnis floscuculi*, *Hydrocotyle vulgaris*, *Filipendula ulmaria*, *Pedicularis palustris*, *Mentha aquatica* and *Potentilla palustris*.

Summarizing these six habitats of subsp. *incarnata*, we see that all are of the nature of marsh, with waterlogged soils with high mineral content and pH between 6·2 and 7·2, the smaller sedges being the usual associates.

In the following six localities in which populations referable to subsp. *coccinea* have been sampled, the habitats are essentially all alike, namely moist slacks in coastal sand-dunes, with stabilized plant cover on 5–10 cm. sandy humus overlying pure sand, the pH at tuber depth ranging from 6·2 (Harlech) to 7·6 (Daliburgh).

C1. Braunton Burrows, North Devon.

In this well-known locality for subsp. *coccinea*, the sample was taken in a dune slack of the most easterly series, about 1 km. inland. There is considerable grazing pressure here, and the vegetation consists of a rather closely nibbled carpet of sedges (*Carex arenaria* and *C. glauca*) and grasses (*Agrostis tenuis, Cynosurus cristatus, Koeleria cristata, Anthoxanthum odoratum* and *Festuca rubra*) with some *Salix repens, Lotus corniculatus, Trifolium repens, Prunella vulgaris, Galium verum*, etc.

C2. Harlech Dunes, Merionethshire.

The subsp. *coccinea* is abundant all over this dune system. The sample was collected in a dune slack *c.* ¾ km. inland, west of the golf course. Grazing is much less heavy than in the Braunton Burrows site, and *Salix repens* is plentiful in the associated vegetation, with great amounts of *Epipactis palustris*. The orchids grow among relatively tall grasses (*Anthoxanthum odoratum, Cynosurus cristatus, Sieglingia decumbens, Koeleria cristata* and *Agrostis tenuis*) with *Potentilla anserina, Ranunculus flammula, Prunella vulgaris, Leontodon leysseri, Anagallis tenella, Equisetum variegatum* and the bottom mosses *Acrocladium cuspidatum, Rhytidiadelphus triquetrus* and *R. squarrosus*.

C3. Budorgan Dunes, Hermon, Anglesea.

This habitat is similar to the last. The marsh orchids occur plentifully in most of the moister hollows throughout the dunes, and although the associated flora closely resembles that at Harlech, there is evidence of considerably greater grazing pressure, and *Epipactis palustris* is rare.

C4. Curracloe Dunes, Co. Wexford.

Subsp. *coccinea* occurs with *D. purpurella* in most of the dune slacks of this extensive system. The sample was taken about ¼ km. inland, in a level-floored depression subject to flooding, in which occasional tussocks of *Juncus acutus* occur. The whole area is lightly grazed.

C5. Tramore Strand, Co. Donegal.

Subsp. *coccinea* is common all over the very extensive stretch of moist, stabilized dune grassland which lies behind the dune system of Tramore Strand. The sample was taken in an area where *Eleocharis palustris, Juncus articulatus* and the smaller sedges are abundant, with *Holcus lanatus, Poa pratensis, Anthoxanthum odoratum, Cynosurus cristatus*, and the usual herbs of moist dune grassland, *Galium verum, Potentilla anserina, Hydrocotyle vulgaris, Ranunculus flammula, Lotus corniculatus, Trifolium repens, Prunella vulgaris*, etc.

C6. Daliburgh Dunes, Isle of South Uist.

The sample was collected from a colony occurring on the moist, level floor of a large blow-out. Throughout most of the area, *Juncus balticus* is abundant in the vegetation, which otherwise has a composition similar to that in the last locality, Tramore Strand, Donegal.

The following population is an example of one which links the subspp. *incarnata* and *coccinea* :

C7. Dune marsh, Bunowen Bay, Co. Galway.

The habitat is practically identical with that of L6, Dooaghtry, Co. Mayo, which is placed above under subsp. *incarnata*, and the associated vegetation is very similar. The individuals range in flower colour between pale flesh-pink and deep crimson-red. The soil-pH at tuber depth in the sampling area was 7·0–7·2.

TABLE II.—Biometrical data for some population samples of *D. incarnata* Floral and vegetative characteristics as listed below.

Locality	Floral Characters					Vegetative characters				
	N	A	B	C	D	N	E	F	G	H
L1 Otterbourne	50	5·34 ± 0·08	6·35 ± 0·09	7·28 ± 0·0	2·46 ± 0·03	29	28·5 ± 0·88	4·75 ± 0·09	13·6 ± 0·44	1·94 ± 0·07
L2 Longstock	50	6·13 ± 0·07	6·92 ± 0·14	7·72 ± 0·10	2·84 ± 0·05	50	27·7 ± 0·61	4·86 ± 0·11	12·17 ± 0·46	1·85 ± 0·05
L3 Pentglas	50	5·35 ± 0·06	6·88 ± 0·10	6·86 ± 0·08	2·75 ± 0·05	50	28·2 ± 0·77	5·55 ± 0·10	10·15 ± 0·27	1·36 ± 0·04
L4 Newcastle	30	6·01 ± 0·09	6·81 ± 0·10	7·24 ± 0·09	2·94 ± 0·06					
L5 Castlegregory	40	5·54 ± 0·09	7·07 ± 0·10	7·35 ± 0·10	3·04 ± 0·04					
L6 Dooaghtry	40	5·72 ± 0·05	7·01 ± 0·09	7·30 ± 0·08	2·50 ± 0·04	50	27·2 ± 0·71	5·06 ± 0·12	9·53 ± 0·22	1·41 ± 0·04
C1 Braunton Burrows	50	6·24 ± 0·06	7·09 ± 0·07	7·81 ± 0·07	2·98 ± 0·04	37	8·6 ± 0·27	4·64 ± 0·09	6·41 ± 0·21	1·42 ± 0·05
C2 Harlech	60	6·04 ± 0·08	7·87 ± 0·10	7·43 ± 0·08	2·92 ± 0·04	50	28·5 ± 0·62	4·85 ± 0·09	10·94 ± 0·22	1·74 ± 0·05
C3 Budorgan	50	5·36 ± 0·07	6·17 ± 0·07	6·40 ± 0·05	2·00 ± 0·04	50	28·3 ± 0·60	4·39 ± 0·07	12·12 ± 0·24	1·34 ± 0·03
C4 Curracloe	65	6·02 ± 0·04	6·82 ± 0·08	6·64 ± 0·07	2·89 ± 0·03	50	11·6 ± 0·41	5·08 ± 0·08	7·36 ± 0·24	1·31 ± 0·04
C5 Tramore	50	6·20 ± 0·07	7·72 ± 0·10	7·50 ± 0·10	2·68 ± 0·05	100	18·6 ± 0·30	5·01 ± 0·07	8·13 ± 0·24	1·40 ± 0·05
C6 Daliburgh	50	5·60 ± 0·08	6·81 ± 0·04	7·28 ± 0·08	2·89 ± 0·05	133	12·3 ± 0·23	4·66 ± 0·05	—	—
C7 Bunowen Bay	50	5·42 ± 0·06	6·76 ± 0·12	7·11 ± 0·06	3·28 ± 0·05	50	26·3 ± 0·60	4 97 ± 0·07	—	—
O1 Blo Norton Fen	50	6·65 ± 0·08	8·81 ± 0·15	8·43 ± 0·09	2·92 ± 0·04	30	45·4 ± 1·56	4·84 ± 0·09	15·30 ± 0·53	1·43 ± 0·07
P1 Hartland Bog	50	6·31 ± 0·07	7·42 ± 0·11	6·74 ± 0·07	3·03 ± 0·06	100	24·6 ± 0 82	4·75 ± 0·08	9·12 ± 0·19	1·44 ± 0·03
P2 Cranes Moor	50	6·41 ± 0 47	7·54 ± 0·13	7·22 ± 0·06	3·46 ± 0·05	50	21·7 ± 0·97	4·54 ± 0·07	11·66 ± 0·37	1·46 ± 0·04
P3 Walton Common	40	6·76 ± 0 05	8·51 ± 0·06	7·07 ± 0·09	3·08 ± 0·04	28	29·3 ± 1·09	4·75 ± 0·08	14·11 ± 0·49	1·59 ± 0·04
P4 Lough Bunny	40	6·78 ± 0 08	7·69 ± 0·11	7·84 ± 0·09	2·97 ± 0·05	50	37·1 ± 0·84	4·55 ± 0·09	10·91 ± 0·33	1·51 ± 0·03
P5 Lough Corrib	50	6·21 ± 0·08	7·77 ± 0·12	7·83 ± 0·09	2·99 ± 0·04	50	34·8 ± 0·83	4·93 ± 0·10	12·31 ± 0·30	1·53 ± 0·05
P6 Conlig	50	6·59 ± 0·07	7·98 ± 0·13	6·88 ± 0·06	3·23 ± 0·06	40	20·6 ± 0·82	4·90 ± 0·10	9·26 ± 0·20	1·28 ± 0·04
P7 Borth Bog	60	5·97 ± 0·09	7·76 ± 0·13	7·39 ± 0·10	2·86 ± 0·05	50	34·2 ± 0·95	4·43 ± 0·10	12·82 ± 0·47	1·80 ± 0·07
P8 Fenor	50	6·08 ± 0·06	6·19 ± 0·10	7·57 ± 0·08	3·03 ± 0·04	50	23·7 ± 0·60	4·65 ± 0·11	12·27 ± 0·30	1·43 ± 0·07
P9 Lough Avaul	50	5·76 ± 0·07	5·89 ± 0·11	6·61 ± 0·07	2·76 ± 0·04	40	21·9 ± 0·60	3·77 ± 0·10	7·44 ± 0·27	0·91 ± 0·03
P10 Creggan Lough	50	6·27 ± 0·06	6·01 ± 0·09	7·20 ± 0·07	2·91 ± 0·05	30	24·7 ± 0·80	4·07 ± 0·08	10·17 ± 0·36	1·21 ± 0·04
P11 Lough Mullaghderg	50	5·55 ± 0·07	6·02 ± 0·07	7·29 ± 0·07	2·50 ± 0·04	30	26·9 ± 1·03	3·87 ± 0·08	8·79 ± 0·25	1·08 ± 0·04
R1 Lough Carra	100	5·82 ± 0·07	6·38 ± 0·10	7·65 ± 0·08	2·91 ± 0·05	94	31·4 ± 1·08	4·69 ± 0·04	9·42 ± 0·26	1·25 ± 0·03

Floral characters :

A, Labellum length (mm.)
B, Labellum width at broadest point (mm.)
C, Spur length (mm.)
D, Spur width (mm.)

Vegetative characters :

E, Overall stature, excluding tubers (cm.)
F, Number of expanded foliage leaves, excluding basal leaf-scales
G, Length of largest leaf, opening of sheath to tip (cm.)
H, Width of largest leaf (cm.)

Biometrical data for samples from the colonies of subsp. *incarnata* and subsp. *coccinea* are recorded in Tables II and III.

The seven samples of subsp. *incarnata* show reasonable homogeneity in labellum patterning, the bulk of individuals in each agreeing with grade 3 of fig. 1, which is the pattern usually attributed to the type form of *D. incarnata*. There is similar agreement between the samples placed under subsp. *coccinea*, grade 3 again being modal. Disruption of the pattern is more frequent, however, and the aggregate shows greater representation of grade 4 than the aggregate of subsp. *incarnata*. Due to the greater intensity of the background coloration, the labellum patterning of subsp. *coccinea* is always much less conspicuous than that of *incarnata*. This no doubt explains Pugsley's statement that the lip of *coccinea* is less well marked than in the type variety.

TABLE III.—Labellum pattern and shape distributions (scored in grades corresponding with those of figs. 1 and 2) in population samples of *D. incarnata*. Percentage to nearest 1 per cent in each group.

Locality	Pattern grades				Shape grades				
	1	2	3	3	1	2	3	4	5
L1 Otterbourne	—	8	86	6	—	2	68	24	6
L2 Longstock	—	4	88	8	—	2	18	50	30
L3 Pentglas	—	7	72	22	—	12	64	18	6
L4 Newcastle	—	—	97	3	—	—	63	20	17
L5 Castlegregory	—	—	67	33	—	—	77	23	—
L6 Dooaghtry	—	8	89	3	—	13	78	7	3
C1 Braunton Burrows	—	—	84	16	—	—	38	44	18
C2 Harlech	—	5	80	15	—	7	38	47	8
C3 Budorgan	—	—	92	8	—	10	58	30	2
C4 Curracloe	—	3	58	38	—	11	43	40	6
C5 Tramore	—	—	86	14	—	—	56	40	4
C6 Daliburgh	—	—	76	24	—	—	68	30	2
C7 Dunowen	—	—	100	—	—	—	50	38	12
O1 Blo Norton Fen	100	—	—	—	62	32	6	—	—
P1 Hartland Bog	—	—	—	100	—	—	8	22	70
P2 Cranes Moor	—	—	—	100	—	—	12	36	52
P3 Walton Common	—	—	100	—	—	—	—	100	—
P4 Lough Bunny	—	8	17	75	—	3	15	50	32
P5 Lough Corrib	—	—	12	88	—	—	22	34	44
P6 Conlig	—	—	—	100	—	—	20	34	46
P7 Borth Bog	—	—	27	73	—	52	35	5	8
P8 Fenor	—	12	18	70	—	—	4	38	58
P9 Lough Avaul	—	58	42	—	—	—	44	42	14
P10 Creggan Lough	24	32	40	4	—	—	14	60	26
P11 Lough Mullaghderg	46	54	—	—	—	—	22	52	26

In labellum shape, the modal class for five of the samples of subsp. *incarnata* corresponds with grade 3 of fig. 2. In one, from Longstock, Hampshire (L2) the modal shape corresponds with grade 4, and some 30 per cent of individuals conform with grade 5. The data for this sample have been included to illustrate the considerable differences which may exist between populations in close geographical proximity, for it contrasts strikingly with the neighbouring L1, near Otterbourne, some 25 miles distant, in this feature.

The modal class for labellum shape in the samples placed under subsp. *coccinea* is again in most cases grade 3. The Braunton Burrows colony, C1, contains a higher proportion of individuals agreeing in labellum shape with grades 4 and 5 than the remainder, and colonies in as close proximity as C2

(Harlech Dunes) and C3 (Budorgan, Anglesea) differ significantly from each other in the representation of these classes. Silhouettes of labella from homologous flowers of samples from colonies C2 and C3 are illustrated in fig. 6.

As in subsp. *incarnata*, the labellum shape differences between the different colonies of subsp. *coccinea* are reflected in differences in ratio of length to width. There are, in addition, considerable differences in absolute size of labella, as is apparent from Table II. The greatest variation is between the neighbouring Harlech and Anglesea topodemes (C2 and C3) ; the sample data suggest that the former exceeds the latter by some 40 per cent in average labellum area.

Neither in labellum shape nor size (fig. 4) can it be said that the samples referred to subsp. *coccinea* differ in the aggregate in any clear cut manner from those placed under subsp. *incarnata*.

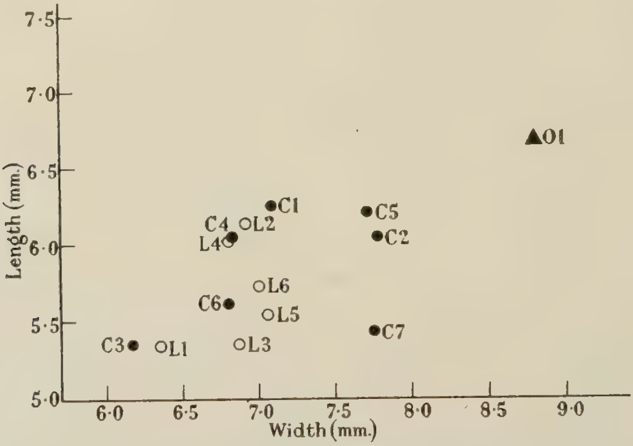

FIG. 4.—Labellum dimensions in samples of subsp. *incarnata* (prefix L), subsp. *coccinea* (prefix C) and subsp. *ochroleuca* (prefix O).

Both groups show considerable variation in spur size (fig. 5), but again there is no appreciable difference between them. Among colonies placed under subsp. *coccinea*, the most striking difference is between the neighbouring C2 (Harlech Dunes) and C3 (Budorgan Dunes, Anglesea), the former of which exceeds the latter by some 27 per cent in mean length and 47 per cent in mean maximum width, to judge from the sample data. This difference is correlated with that in labellum dimensions noted above.

Sample data for stature and leaf number are given in Table II. There is remarkably little difference between the colonies of subsp. *incarnata* in average stature, nor is there great variation among them in average number of leaves. In those of subsp. *coccinea*, whilst variation in leaf number is relatively slight, that in stature is quite considerable. The association between plant stature and the height of neighbouring vegetation is clearly a very close one. The smallest sample mean, 8·6 cm., is that of C1, from Braunton Burrows ; the largest, 28·5 cm., that of C2, from Harlech Dunes. All of the fifty plants in flower collected from the latter locality—where grazing is slight—were intact, while thirteen of the sample of fifty from Braunton Burrows, where grazing is intense in the sample area, were rejected because of damage to leaves or spike. The figure for mean stature in the latter case thus refers to the portion of the sample not curtailed by grazing animals, and it is therefore a biased estimate. Clearly the selection in favour of dwarf habit must be considerable in heavily grazed sites. It may be noted that there is no obvious connection between overall plant size and flower dimensions. In every flower dimension the Braunton Burrows sample, C1, considerably exceeds that from Budorgan Dunes, C3, although it is less than one third of the average stature.

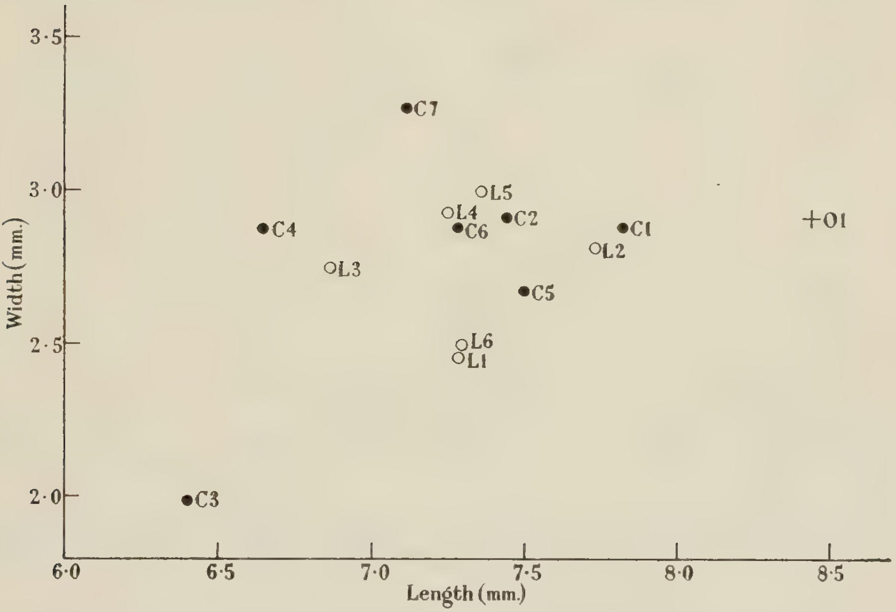

FIG. 5.—Spur (nectary) dimensions in samples of subspp. *incarnata*, *coccinea* and *ochroleuca*. Coding as in fig. 4.

Sample data for dimensions of the largest leaf are given in Table II. As is to be expected, the smallest average leaf length occurs in the dwarf colonies of the subsp. *coccinea*, C1 (Braunton Burrows), C4 (Curracloe) and C5 (Tramore). The difference in leaf length between these and the taller colonies such as C2 (Harlech) and C3 (Budorgan) is by no means in proportion to the difference in stature. In C1, the ratio of length of largest leaf to overall stature is 0·74 : 1 ; in C2, 0·45 : 1. The ratio of leaf length to stature in the latter is of the same order as in the colonies of subsp. *incarnata*. Leaf width in the dwarf colonies of subsp. *coccinea* is not appreciably less than in the taller colonies referred to this subspecies, nor than in those of subsp. *incarnata*.

The foregoing analysis suggests that the flower-colour difference upon which the grouping of the colonies under the two subspecies, *incarnata* and *coccinea*, is based, is not correlated with any other floral differentiae of a clear-cut nature. A small difference in the composition of the samples in respect to labellum patterning has been demonstrated, one which, in itself, would be of little taxonomic significance. In labellum and spur shape and size, the variation within each group is considerable, and certainly these characters do not serve to differentiate the two.

The variation in vegetative organization is of some interest, however. As has been shown, some of the populations of subsp. *coccinea* correspond closely with those of subsp. *incarnata* in stature, and in the number and size of leaves. Others occurring in habitats where associated vegetation is of small stature (usually as the outcome of grazing) differ considerably in habit. Three factors contribute to the characteristic appearance of these dwarf colonies : firstly,

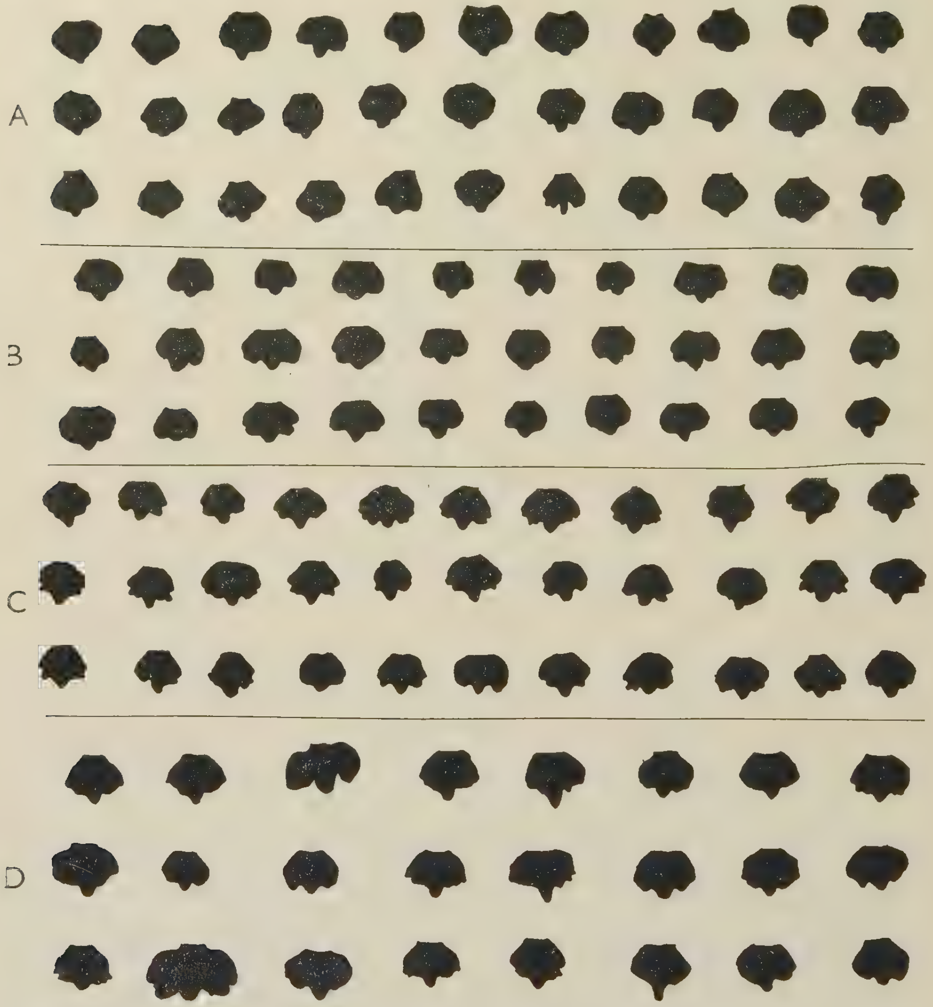

FIG. 6.—Silhouettes of labella of homologous flowers from population samples of *D. incarnata*. A, subsp. *incarnata*, L2 (Longstock); B, subsp. *incarnata*, L3 (Pentglas); C, subsp. *coccinea*, C3 (Budorgan); D, subsp. *coccinea*, C2 (Harlech). All ×*c*. 1.

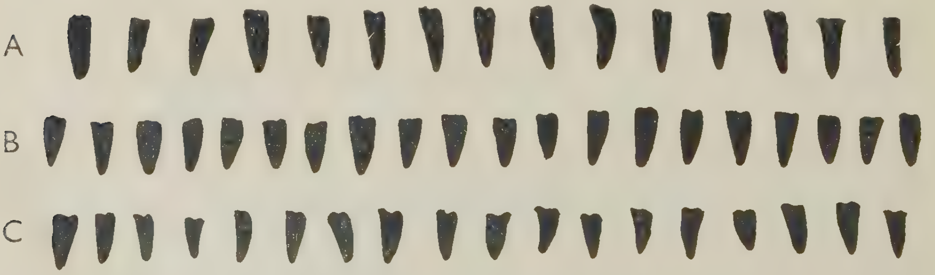

FIG. 7.—Silhouettes of spurs from labella of *D. incarnata*. A, subsp. *incarnata*, L2 (Longstock); B, subsp. *incarnata*, L3 (Pentglas); subsp. *coccinea*, C3 (Budorgan). All ×*c*. 1.

the leaves are, on the average, no fewer in number than in the taller colonies so that average internode length is less ; secondly, the ratio of leaf length to stem length is substantially greater, and thirdly, the leaves are, on the average, somewhat broader in relation to their lengths. Pugsley's description of *coccinea*, " plant usually dwarf, with upper leaves sometimes exceeding the spike " has thus some justification in application to these colonies.

The relationship of the subspp. *incarnata* and *coccinea* cannot be considered without reference to their habitat preferences, for these are rather distinctive. The six colonies of subsp. *incarnata*, compared above, all occur in marsh habitats; the seven of subsp. *coccinea*, all in dune slacks. These may be said to be the characteristic habitats of the two.

It is true that the colonies L5 (Castlegregory) and L6 (Dooaghtry), referred to subsp. *incarnata* because of their prevailing flower colour, occur in dune marshes, and in this connection the colony C7 (Bunowen) is of interest, for the habitat of this is of the same nature. The variation in flower colour in this colony is such that it cannot be associated justifiably with either of the subspecies on this basis alone. In no other floral features, however, does this Bunowen colony show excessive variation—the labellum pattern is, in fact, unusually invariable in the sample, corresponding uniformly with grade 3. The sample data suggest that in labellum shape, and in average stature and leaf number, the colony is in good agreement with others placed under subsp. *incarnata*, including L5 (Castlegregory) and L6 (Dooaghtry) occurring in similar habitats in other parts of the western Irish seaboard. There is a discrepancy in mean spur width, since the sample mean considerably exceeds that of others referable to subspp. *incarnata* and *coccinea*. Another curious characteristic of this and similar colonies in western Connemara, not observed outside of this area, is that in almost every inflorescence the lowest two or three bracts do not subtend flowers, nor even a trace of a flower bud.

The type of flower colour distribution in the Bunowen colony C7 is to be found in several in coastal areas in western Scotland and Ireland. Most of these, like the Bunowen colony, occur in dune marshes, and agree in general facies with the usual marsh form of subsp. *incarnata* in all but uniformity of flower colour. In one or two, as in the Rosses, Co. Donegal, the habitat is drier dune slacks, and the general facies of the plants is more reminiscent of " typical " (i.e. dwarf) subsp. *coccinea*.

Subsp. *pulchella*.

The colonies placed under this subspecies occur in habitats which can be classified very roughly in three groups : A, *Schoenus nigricans* fen or marsh, with fairly strong mineral flushing, soil-pH 6·2–7·5 ; B, poor fen, with soil-pH 5·2–6·8, *Schoenus* and *Sphagnum* spp. both absent or unimportant, and C, soligenous bog, with soil–pH 5·0–6·0 and a more or less complete carpet of the less oxyphilous *Sphagnum* species.

P1. Hartland Bog, nr. Wareham, Dorset.

The sample was taken in the southern arm of this bog, in an area where *Schoenus* is dominant with *Molinia caerulea* an important associate. *Carex flacca*, *C. hostiana*, *C. panicea*, *Eriophorum angustifolium*, *Lythrum salicaria* and *Cirsium dissectum* also occur in some abundance in this area, on blackish peat with a pH *c.* 6·8.

P2. Cranes Moor, New Forest, Hampshire.

The sample was collected in an area where tussocky *Schoenus* is abundant, with much *Phragmites* and *Juncus sylvaticus*. Associated species include

Molinia caerulea, Eriophorum angustifolium, Carex nigra, C. echinata, Cirsium dissectum, Narthecium ossifragum and locally *Sphagnum palustre* and *S. papillosum*. The pH of the soil-water in the sample area was *c.* 6·4.

P3. East Walton Common, Norfolk.

Small patches of fen in which *Cladium* is dominant are scattered over most of this common, interspersed with drier areas bearing meadow vegetation and level stretches of *Schoenus* fen. The sample was collected in the latter, associated plants including *Cladium, Phragmites, Juncus subnodulosus, Eriophorum latifolium, Carex flacca, C. hostiana, C. lepidocarpa, C. nigra, C. panicea, Molinia caerulea, Eupatorium cannabinum, Cirsium dissectum* and the mosses *Acrocladium cuspidatum, Ctenidium molluscum, Drepanocladus revolvens* and *Campylium stellatum*. Soil-pH was *c.* 7·0.

P4. Lough Bunny, Co. Clare.

The sample was collected in a stretch of *Schoenus*-dominated fen north east of the Lough. In this area, *Phragmites* and *Cladium* are abundant, with *Juncus subnodulosus, Carex lasiocarpa, C. panicea, C. nigra, C. hostiana, C. flacca, Cirsium dissectum, Molinia caerulea,* etc. Like the plants of *D. traunsteineri* which also occur here in small numbers, the plants of *D. incarnata* were rooted loosely in a moss carpet composed mostly of *Ctenidium molluscum, Cratoneuron commutatum* and *Acrocladium cuspidatum*. pH of the soil water was *c.* 7·4.

P5. Fen, S.E. shore, Lough Corrib, Co. Galway.

This habitat is practically identical with the foregoing, lake margin fen, with a dominance of *Schoenus,* and some *Cladium, Phragmites* and the smaller sedges. The colony is of interest as being on the margin of an area where intergradation with subsp. *cruenta* is apparent ; no leaf-marked individuals were found in it, however.

The foregoing five colonies fall in ecological group A.

P6. Marsh at Conlig, Co. Down.

This habitat differs from the foregoing in the absence of *Schoenus nigricans*. The orchids grow in a sedge meadow in which *Carex rostrata, C. nigra, C. panicea* and *C. flacca* are abundant, with *Phragmites, Juncus sylvaticus, Eleocharis palustris, Menyanthes trifoliata, Lychnis floscuculi, Hydrocotyle vulgaris, Hypericum elodes,* etc. Bottom mosses include *Acrocladium cuspidatum, Drepanocladus revolvens* and, locally, *Sphagnum squarrosum* and *S. palustre*. The pH of the soil water in the sample area was *c.* 6·8.

P7. Borth Bog, Cardiganshire.

This bog has been drained and extensively cut for peat, and no marsh orchids now occur on the drier areas. Throughout the wetter parts, which show various stages of recolonization by bog vegetation, a purple-flowered form of *D. incarnata* is plentiful. The sample was taken in an area of tall, open *Phragmites*, where associated vascular species include *Molinia caerulea, Juncus effusus, Myrica gale,* etc. *Sphagnum palustre, S. papillosum* and *S. contortum* occur locally. Soil-pH was *c.* 5·2.

P8. Marsh nr. Fenor, Co. Waterford.

D. incarnata occurs here in sedge meadow with *D. purpurella*. The main associated species are *Phragmites, Carex rostrata, C. nigra, C. panicea, C. flacca,*

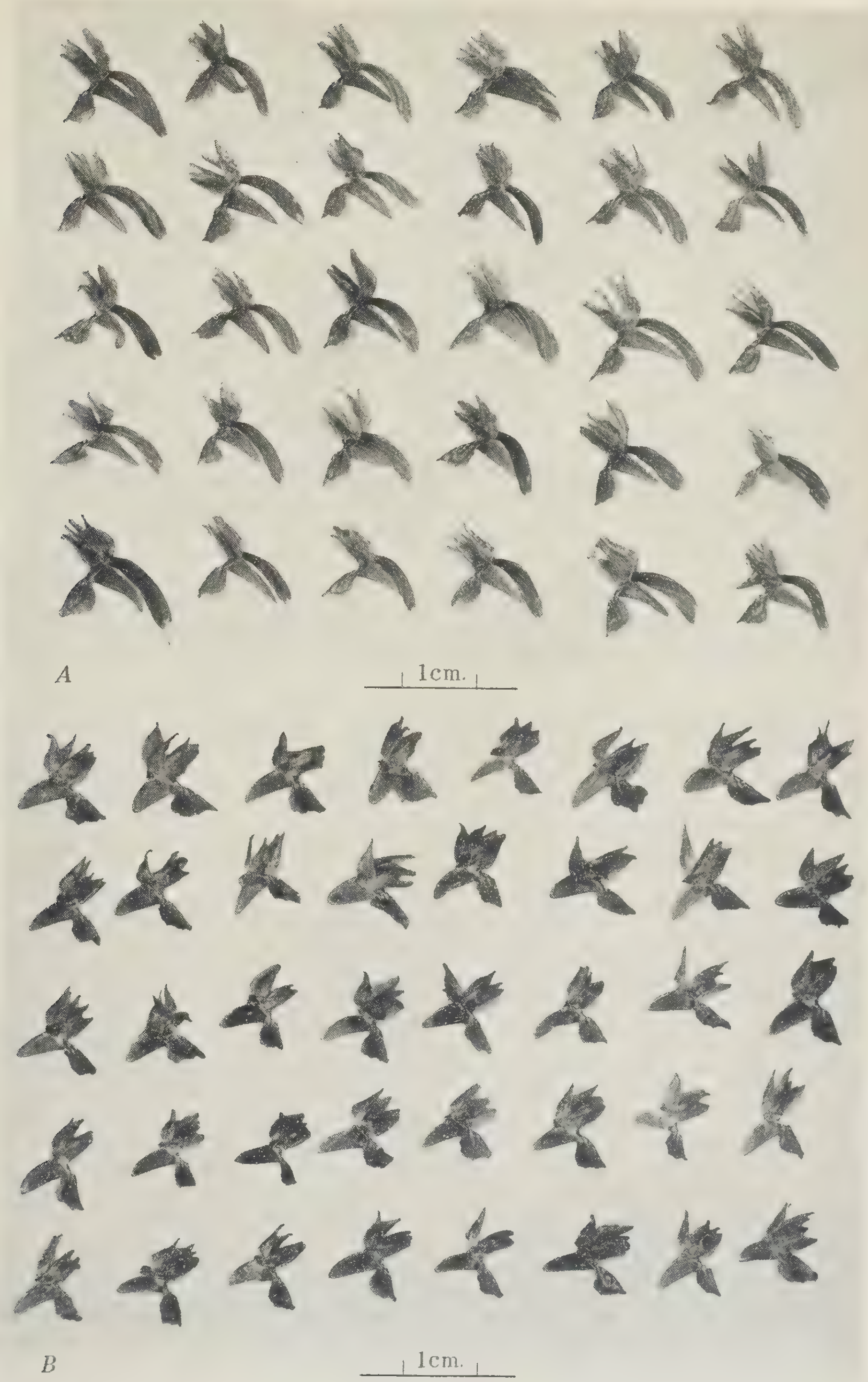

Plate I.

Homologous flowers from population samples of *D. incarnata* to illustrate differences in spur shape.

A. 30 plants of subsp. *incarnata* (Otterbourne, Hants.).

B. 40 plants of subsp. *pulchella* (Hartland Bog, Dorset). The ovaries have been removed from these flowers.

Eriophorum angustifolium, Eleocharis multicaulis, Equisetum fluviatile and *Potentilla palustris*; *Carex paniculata* is also present, and *Typha latifolia.* The mosses *Acrocladium cuspidatum* and *Aulacomnium palustre* are abundant. Soil-pH was *c.* 5·8.

The foregoing three colonies fall in ecological group B.

P9. Bog near Lough Avaul, W. of Glengariff, Co. Cork.

The sample was collected in marginal bog where the orchids grow in a carpet of *Sphagnum* spp., mostly *S. papillosum, S. girgensohnii* and *S. magellanicum*, with *Eriophorum angustifolium, Molinia caerulea, Erica tetralix, Narthecium ossifragum,* and *Pinguicula grandiflora. Schoenus* is present in small quantity, and in the wetter zones, *Carex limosa* is abundant with *Menyanthes trifoliata*. Soil-pH was *c.* 5·0.

P10. Creggan Lough, nr. Westport, Co. Mayo.

The sample was collected in a bog at the south end of the lake, where *D. purpurella* occurs in about equal numbers. *Carex rostrata* and *C. lasiocarpa* are present in the sample area, with *Equisetum fluviatile, Juncus sylvaticus* and *J. effusus, Filipendula ulmaria, Myrica gale, Molinia caerulea, Potentilla palustris, Hypericum elodes, Apium nodiflorum,* etc. *Sphagnum* species present in the sample area include *S. palustre, S. papillosum* and *S. acutifolium*. Soil-pH was *c.* 5·6.

P11. Lough Mullaghderg, Co. Donegal.

The sample was collected in marginal bog at the south west end of this lough, in an area where the smaller sedges, *Carex nigra, C. flacca, C. echinata* and *C. serotina* form the main vegetation, with *Phragmites, Juncus sylvaticus, Equisetum fluviatile, E. palustre, Menyanthes trifoliata, Mentha aquatica, Hydrocotyle vulgaris,* etc. The *Sphagnum* species *S. palustre* and *S. papillosum* are locally abundant, and *Acrocladium cuspidatum* is also present. Soil-pH was *c.* 5·4.

The last three colonies form ecological group C.

Sample data for morphological features are recorded in Table II. There is considerable diversity, both in mean expression of the various attributes and in the internal variability of the different colonies. Since the samples were in all instances culled from uniform habitats, ecologically conditioned variation within them should be at a minimum, and differences in sample variability are likely to reflect differences in genetical heterogeneity of the colonies. The least variable colony is that on Walton Common, and the most variable, that in Borth Bog. The coefficients of variation in labellum width and spur length are, for the former sample, 4·3 per cent and 7·6 per cent, and for the latter, 12·9 per cent and 10·2 per cent. The two colonies are about equally variable in stature, the former with a coefficient of variation of 19·7 per cent for this feature, and the latter, 19·8 per cent. The narrow range of variation in the Walton colony P3 is seen also in labellum shape and patterning (Table III); all individuals of the colony conform to a single standard in both of these features. In fact, in floral features, the overall variation in all of the individuals of this colony examined does not transcend that commonly to be found between the different flowers within a single inflorescence.

The morphological variation between the different topodemes is such that no really clear-cut division into subgroups is possible. It is, however, instructive to enquire how far habitat differences are reflected in morphology.

The distribution of the broad ecological groups, A (P1, P2, P3, P4 and P5), B (P6, P7 and P8) and C (P9, P10 and P11) in labellum dimensions is indicated in fig. 8, and in spur dimensions, in fig. 9.

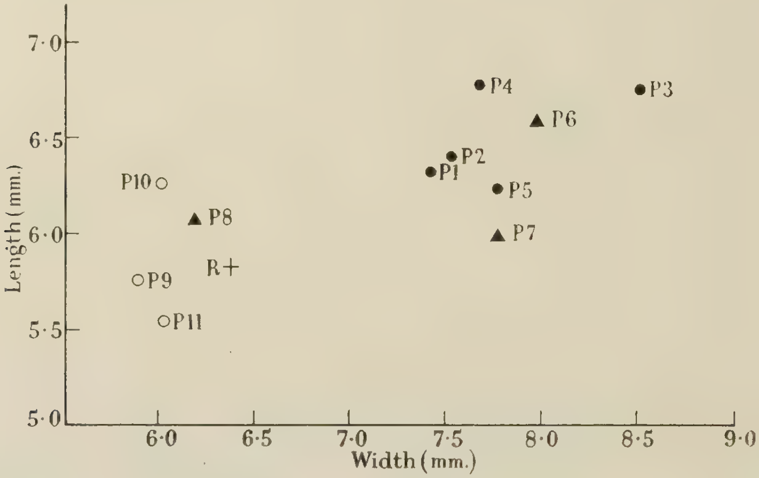

FIG. 8.—Labellum dimensions in samples of subspp. *pulchella* and *cruenta*. P1–5, ecological group A ; P6–8, ecological group B ; P9–11, ecological group C ; R, subsp. *cruenta*.

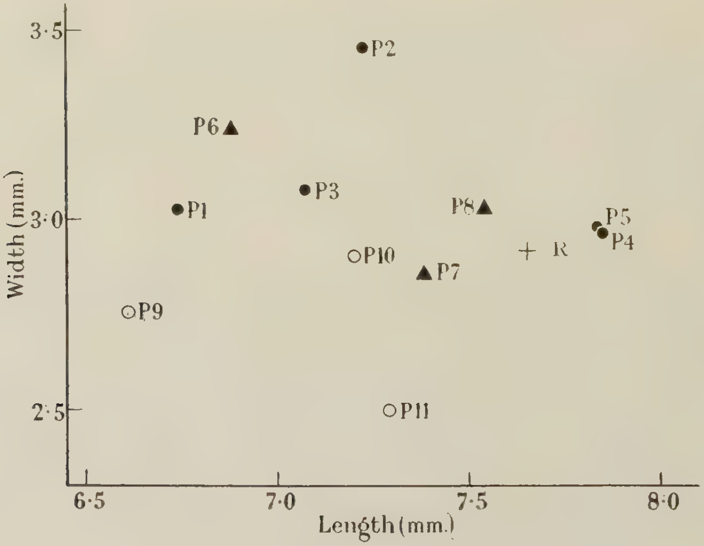

FIG. 9.—Spur dimensions in samples of subspp. *pulchella* and *cruenta*. Coding as in fig. 8.

The distinction between group A and group C in labellum width is obviously highly significant. Two of the colonies in group B, P6 and P7, fall within the range of group A, and one, P8, within that of group C. It is interesting to note that the sample R1 of subsp. *cruenta* falls between the two groups, although this colony occupies a habitat similar to those of group A. A similar but less marked trend of differentiation between the three groups is apparent in spur dimensions.

There is a further slight correlation with vegetative features. In mean width of largest leaf (fig. 10), the samples from the colonies of group A all exceed those of group C, and all but P1 of the former group exceed those of group C in leaf length also. Similarly, in average leaf number and stature the sample data suggest that the colonies of group A exceed those of group C. In all of these vegetative features, the colonies of the 'intermediate' group, B, show a somewhat scattered distribution, mostly, however, falling in the neighbourhood of the *Schoenus* bog series, group A.

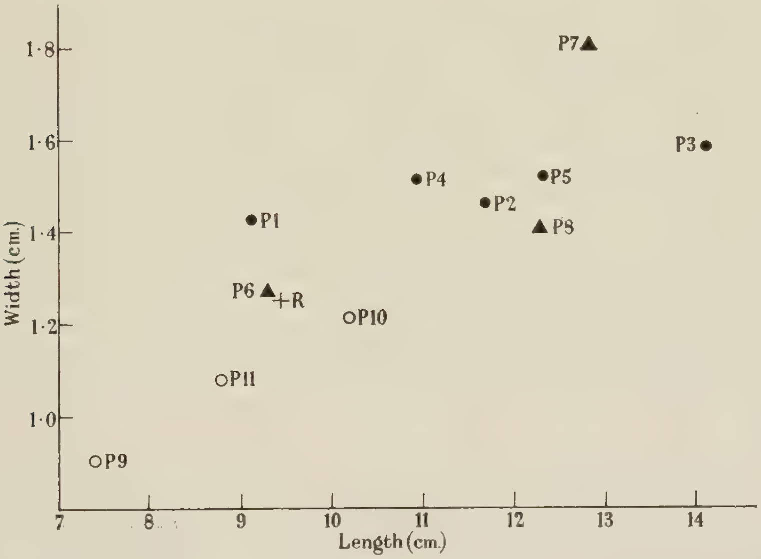

Fig. 10.—Leaf dimensions in samples of subspp. *pulchella* and *cruenta*. Coding as in fig. 8.

Turning to the variation within the ecological groups for other floral characteristics than linear dimensions, we find additional evidence of regularity.

Group A. In labellum patterning (Table III), the samples P1 (Hartland Bog) and P2 (Cranes Moor) are in agreement in the 100 per cent representation of pattern grade 4. The New Forest is the type area of the subsp. *pulchella* (Druce, 1917 ; Pugsley, 1935), and it may be noted that Pugsley's description of the labellum patterning in this form, 'strongly variegated with darker lines', is fitting enough for grade 4 of fig. 1. This grade is predominant also in the samples P4 and P5, but not in P3, for the uniform Walton Common colony, in which all of the plants examined conformed with pattern grade 3.

In labellum shape, the samples P1 and P2 are again in general agreement in the dominance of shape grade 5 ('lip subentire', Puglsey, 1935). P5 corresponds to some extent, although grade 3 is more heavily represented. Grade 4 is modal in P4, but one third of the plants still conform in labellum shape with grade 5. The Walton Common colony, P3, again differs from others of the group, here in the conformity of all its members to grade 4 in labellum shape.

Group B. The sample data suggest that in labellum patterning all of the colonies in this group agree in the dominance of pattern grade 4, characteristic, as we have seen, of most of those of group A. Two of this group, P6 and P8, are also in agreement with most of those of group A in the dominance of labellum shape grade 5. One departs considerably in this feature, P7, Borth Bog, in the sample from which shape grade 2 is modal.

Group C. In labellum patterning, the three colonies placed in this ecological group evidently differ markedly from those of the two foregoing. The sample data suggest that the majority of individuals agree in labellum patterning with grades 1 or 2, i.e., they possess lips which are either concolorous, or marked only with a pattern of fine dots. In P11, from Donegal, no individuals at all show a distinct labellum pattern of lines or bars ; in the other western Irish colonies, P9 and P19, however, a substantial proportion of individuals exhibit labellum patterns similar to grade 3.

In two of the colonies of group C, labellum shape grades 4 and 5 appear to dominate ; in the third, P9, grade 3 is more heavily represented.

As previously made clear, the grouping of these eleven topodemes under subsp. *pulchella* has been based simply upon prevailing flower colour—magenta-purple in all. It will be obvious from the above analysis that the assemblage is homogeneous in relation to no other phenotypic feature of those which have been studied. Nevertheless, it remains a fact that none of these individual topodemes possesses a combination of floral characters, flower colour excluded, which would bring it into good agreement with, say, subsp. *incarnata* or subsp. *coccinea*. Even the Walton Common population, P3, which, in labellum patterning, vegetative features and floral dimensions agrees reasonably well with subsp. *incarnata*, is unique as a population in the uniform occurrence in it of a labellum shape conforming with grade 4. It may be added that the absence of strong lateral reflexing of the labellum in life gives this remarkably uniform population a quite characteristic facies.

If the Walton Common topodeme, P3, and the rather anomalous P7, Borth Bog, are excluded, the remainder fall roughly into an ecocline, the habitat sequence :

Schoenus bog, poor fen, soligenous bog with
soil-pH 6·4–7·4 ——→ soil-pH 5·8–6·8 ——→ less oxyphilous *Sphagna*,
soil-pH 5·0–6·0

being correlated with a gradient in certain morphological features ; in decreasing stature and leaf size, in decreasing size of floral parts, and in the reduction of the intensity of labellum patterning. Certainly the topodemes which lie at the ' ends ' of this ecocline are well differentiated in these features, notwithstanding the morphological diversity of intermediates.

The Borth Bog colony is of some interest, since this is one of the type localities of Pugsley's var. *cambrica*, the other mentioned in the original description being Tregaron Bog. In a search made over the latter in June 1952, no forms of *D. incarnata* whatever were encountered, so no comment is possible in regard to the population present, or formerly present, there. In dune marshes in Anglesea and on the coast near Aberystwyth, small numbers of a purple-flowered form of *D. incarnata* were seen during 1952 which agreed in general facies, in particular labellum shape and patterning, with those of the Conlig colony, P6, rather than with those in Borth Bog. The plants in the latter locality are highly variable, but the colony as a whole differs in average labellum shape from all others placed under subsp. *pulchella* (fig. 11). It may be noted in passing that except in respect to flower colour, hardly a single statement in Pugsley's description of var. *cambrica* (p. 52) fits the Borth colony either in reference to stature, lip shape and size, or spur size. Presumably this description was based upon small numbers of dried plants in herbaria, since Pugsley's account of the variety appeared thirty years after his collection of specimens from Borth.

Subsp. *cruenta*.

R1. Keel Bridge, Lough Carra, Co. Mayo.

The population in this locality has been described in detail elsewhere (Heslop-Harrison, 1950). The habitat is broadly similar to those of subsp. *pulchella* colonies placed in ecological group A above—highly calcareous lake-side marsh, with dominance of *Schoenus nigricans*. Associated vegetation includes *Juncus subnodulosus*, *Lythrum salicaria*, *Cirsium dissectum*, *Cladium mariscus*, *Pinguicula vulgaris*, *Samolus valerandi*, *Anagallis tenella*, etc. Soil-pH at tuber depth is 8·2–8·4.

Biometrical data for this colony are included in Table II. Although the labellum dimensions are somewhat less than the average in the subsp. *pulchella* colonies occurring in similar habitats (fig. 8), there is no doubt that in the various metrical features recorded, this sample of subsp. *cruenta* falls well within the total range of variation encompassed by the populations placed under subsp. *pulchella*. The principal distinction lies, in fact, in the quite unique pigmentation of the vegetative parts in some 65 per cent of the individuals of the colony. In these the leaves are more or less heavily marked with spots, blotches or fields of reddish purple pigment on both surfaces, and the upper parts of the stem and bracts of the inflorescence are correspondingly pigmented, either over the entire surface or locally in flecks and striations. The flower colour is similar to that of the various subsp. *pulchella* forms, but in the pigmented individuals the background tone of the labellum is somewhat more dilute, lilac instead of magenta-purple, so that the pattern is more conspicuous.

Colonies with the characteristics of this occur at several points around Lough Carra and Lough Mask, and also on the north-east shores of Lough Corrib. Away from this area, in both Galway and Clare, small numbers of leaf-marked individuals appear in similar habitats among populations otherwise simply referable to subsp. *pulchella* ; there is thus, in effect, a complete intergradation between the two subspecies.

Subsp. *ochroleuca*.

O1. Blo Norton Fen, Norfolk.

The orchids here are thinly dispersed through dense reed-swamp composed of *Phragmites*, *Cladium* and *Juncus subnodulosus* growing on thick peat with a pH *c.* 7·5. *Schoenus* nigricans is present, with *Eupatorium cannabinum*, *Carex elata* and smaller sedges.

This is the station for subsp. *ochroleuca* discussed by Pugsley (1939), and it is one of the few in Britain where a practically pure population exists in which the characteristics attributed to subsp. *ochroleuca* on the Continent (e.g. by Fischer and Nelson, 1931) are fully expressed. These characteristics include, apart from the striking flower colour, a broad, strongly three-lobed labellum and large spur (Table II, figs. 4, 5 and 13). Plants of similar facies occur sporadically in neighbouring fens, with other forms of *D. incarnata*, and similar flower colours reappear in populations of the species throughout East Anglia, usually not in association with the larger three-lobed labellum (see colony M3 described below).

POLYMORPHIC.

M1. Doohyle Lough, nr. Rathkeale, Co. Limerick.

D. incarnata is abundant in a field of *c.* 3 acres at the south end of this lough. The field is traversed by an old drainage system, and in the hollows of this wet-soil vegetation prevails, a continuation, in effect, of the lake-side fen. *Schoenus nigricans* is dominant, with *Carex nigra*, *C. disticha*, *C. panicea*, *C. flacca* and some *Cladium*, *Phragmites* and *Iris pseudacorus*. The ridges carry a grassy vegetation, mainly *Cynosurus cristatus*, *Festuca rubra*, *Anthoxanthum odoratum*, *Sieglingia decumbens* and *Holcus lanatus*. These different habitats alternate at intervals of 3–4 m. The drier mineral soil on the ridges and the saturated peaty soil in the hollows showed a similar pH range, 6·5–7·0.

In the narrow belt of *Cladium*- and *Schoenus*-dominated marsh around the margin of the lough, the prevailing form of *D. incarnata* is purple-flowered and corresponds to subsp. *pulchella*. A similar form occurs in the hollows of the drainage system for about 100 m. from the lake margin ; on the drier ridges between these hollows a form corresponding in flower colour to subsp. *coccinea* occurs.

Using the presence of *Schoenus* as a boundary marker between the ' ridge ' and ' hollow ' habitats, one hundred individuals were scored for flower colour in each over a distance of *c.* 30 m. On the ridges, 85 per cent were *coccinea*-like, 15 per cent *pulchella*-like ; in the hollows, the proportion was 4 per cent to 96 per cent. Thus while the two forms are not completely vicarious in this locality, they show clear ecological differentiation.

For the investigation of correlation of other characters, samples of fifty individuals of each of the two colour forms were taken. These were both taken from the ' ridge ' habitat, i.e. on dry soil outside the area of occurrence of *Schoenus*, with the object of eliminating to some extent variation imposed directly by habitat difference.

The distribution of the labellum pattern and shape grades in the two samples is given in Table IV.

TABLE IV.—Labellum pattern and shape distributions (scored in grades corresponding to those of figs. 1 and 2) in two samples of *D. incarnata* from colony M1, Doohyle Lough, Co. Limerick.

Sample	Pattern grades				Shape grades				
	1	2	3	4	1	2	3	4	5
pulchella-like	–	10	4	36	–	—	12	14	24
coccinea-like	–	3	40	7	1	11	29	9	—
	$P<0·05$				$P<0·05$				

Data for the two samples relating to other morphological features are given in Table V. These data suggest while the two colour groups do not differ significantly from each other in labellum and spur dimensions or in leaf number, they are significantly different in stature and leaf dimensions.

Difference in flower colour is thus correlated with other morphological differences in this Rathkeale colony. Comparing the two forms with monomorphic populations placed under the subspp. *pulchella* and *coccinea* which they match in flower colour, we see that there is some degree of agreement. The labellum shape and pattern distributions of the *coccinea*-like portion can be matched in several of the topodemes placed under that subspecies, and these plants would not be out of place among the latter in respect to stature and the

TABLE V.—Biometrical data for two samples of 50 individuals from colony M1, Doohyle Lough, Co. Limerick.

Character	*pulchella*-like	*coccinea*-like	Significance of difference
Stature (cm.)	30·10±0·89	22·20±0·83	<0·05
Leaf number	4·56±0·09	4·83±0·08	>0·05
Leaf length (cm.)	12·43±0·21	10·04±0·35	<0·05
Leaf width (cm.)	1·50±0·05	1·31±0·04	<0·05
Labellum length (mm.)	5·83±0·08	5·83±0·07	>0·05
Labellum width (mm.)	6·46±0·11	6·38±0·09	>0·05
Spur length (mm.)	6·97±0·08	6·84±0·10	>0·05
Spur width (mm.)	3·00±0·04	2·89±0·04	>0·05

dimensions of vegetative and floral parts. The labellum shape distribution in the *pulchella*-like portion resembles that in the colonies P5 (L. Corrib) and P6 (Conlig) placed under subsp. *pulchella*, and the unusual labellum pattern distribution corresponds with that in colony P8 (Fenor), with which there is also resemblance in stature and leaf and labellum dimensions.

From the taxonomic point of view, there would thus appear to be every justification for looking upon the Rathkeale colony as being simply a mixture of two taxonomic subspecies, *pulchella* and *coccinea*, the individuals of which, even within this small area, show a degree of ecological specialization. Broader biological problems are, however, raised by the co-existence of these two, presumably interfertile, groups (Heslop-Harrison, 1953).

It may be noted in passing that on the limestone plain of central Ireland dimorphic populations of *D. incarnata* are not uncommon in suitable localities, usually on the shores of lakes. On the western shore of Lough Ree, for example, a mixed population similar to that described above extends thinly over a distance of several miles. At Hodson's Bay, Co. Roscommon, the two colour groups show a similar ecological differentiation to that observed at Rathkeale, the *pulchella*-like individuals occurring almost invariably in association with *Schoenus*, and the *coccinea*-like plants in drier habitats, even where the habitats alternate within a distance of a few metres. The modal grades for the *pulchella*-like group here are : for labellum shape, 4 and 5, for labellum pattern, 4 ; and for the *coccinea*-like group : for labellum shape, 3, and labellum pattern, also 3.

M2 Redgrave. Middle Fen, South Lopham, Norfolk.

Extensive drainage and frequent burning have very largely destroyed the natural vegetation of this large area of fen and replaced it by a mosaic of seral communities. Part is still covered with groves of *Cladium* on relatively dry, mineral rich peat with a pH *c.* 6·8. Elsewhere *Schoenus* dominates, abundant associates being *Molinia caerulea*, *Juncus sylvaticus*, *Carex flacca*, *C. panicea* and *Phragmites*. Oxyphilous species occur locally, including *Eriophorum angustifolium* and *Drosera rotundifolia*. The alternation is seen also in the mosses, *Ctenidium molluscum*, *Drepanoclados revolvens*, *Campylium stellatum* and *Acrocladium cuspidatum* giving place locally to *Aulacomnium palustre* and *Sphagnum palustre*.

Three flower-colour forms of *D. incarnata* are present in this ecologically rather diverse habitat, (*a*) purple (Séguy 58), (*b*) flesh pink (Séguy 19) and (*c*) yellowish white (slightly lighter than Séguy 270). In this instance, the purple-flowered forms predominate, and there is little variation in flower colour intensity amongst the flesh pink individuals. Those with yellowish white flowers match in this character the colony of subsp. *ochroleuca* in Blo Norton Fen (O1), some 2½ miles distant.

The sample collected from this locality totalled 80 plants ; of these, 50 were purple flowered, 17 yellowish white and 13 flesh pink. The three colour classes are compared for labellum patterning and shape in Table VI.

TABLE VI.—Labellum pattern and shape distributions (scored in grades corresponding with those of figs. 1 and 2) in a sample of *D. incarnata* from colony M2, Redgrave Middle Fen, Norfolk.

Flower colour	Pattern grades				Shape grades				
	1	2	3	4	1	2	3	4	5
(*a*) purple	—	3	34	13	1	11	24	13	1
(*b*) yellow-white	17	—	—	—	—	5	9	3	—
(*c*) flesh pink	—	—	11	2	—	2	10	1	—

In the plants with yellowish white flowers, the labellum is, of course, concolorous, since the genetic system governing the anthocyanin patterning of the labellum must be hypostatic to the gene or genes inhibiting the formation of anthocyanin pigment. In labellum shape, these plants obviously do not differ significantly from the coloured ones in this population; in spite of their agreement in flower colour, they do *not* correspond with subsp. *ochroleuca* in the possession of tri-lobed labella conforming with shape grade 1.

TABLE VII.—Labellum and spur dimensions in a sample of *D. incarnata* from colony M2, Redgrave Middle Fen, Norfolk, with analysis of variance.

Flower colour	Labellum		Spur	
	Length (mm.)	Width (mm.)	Length (mm.)	Width (mm.)
(*a*) purple	5·88±0·08	7·68±0·31	7·68±0·10	3·04±0·049
(*b*) yellow-white	5·51±0·09	6·91±0·14	7·91±0·13	3·34±0·067
(*c*) flesh pink	5·71±0·11	7·23±0·22	7·59±0·21	3·06±0·068
Mean Square:				
between groups (2 degrees of freedom)	14·043	66·461	13·941	9·320
Within a group (77 degrees of freedom)	4·561	11·824	8·305	2·375
Variance ratio (F)	3·075	5·623	1·677	3·923

For P=0·01, F=4·98 For P=0·05, F=3·15

Between the other two flower colour groups, purple and flesh pink, there is no significant difference in the distribution either of labellum patterning or shape.

An analysis of variance for the dimensions of labellum and spur in the three flower colour groups is given in Table VII. There is significant variation between the groups in labellum width and spur width; in each it is the ochroleucous group which deviates. The plants of the latter group evidently possess narrower labella and broader spurs than those with anthocyanin pigmented flowers.

M3. Sutton Broad, Norfolk.

D. incarnata is abundant in fens and marshes throughout the Broads district of Norfolk, where most of the larger colonies appear to be highly polymorphic. A colony on the north side of Sutton Broad was selected for detailed investigation. The vegetation here is typical of that fringing most of the Broads. Tall reed-swamp with *Phragmites*, *Typha angustifolia*, *Equisetum fluviatile*, etc., extends back from the open water for a distance of 15 to 50 m., where it is replaced by sedge meadow on mineral-rich fen peat with a pH 7·0–7·4. The orchids occur in this sedge meadow, which is floristically very rich. More than fifty vascular species were listed in the sample area. Among the most abundant are *Phragmites*, *Carex lasiocarpa*, *Juncus subnodulosus*, *Iris pseudacorus*, *Filipendula ulmaria*, *Eupatorium cannabinum*, *Rumex hydrolapathum*, *Lythrum salicaria*, *Epilobium hirsutum*, *Cicuta virosa*, *Oenanthe fistulosa*, *Valeriana officinalis*, *Lycopus europaeus* and *Menyanthes trifoliata*. Bryophytes present include *Acrocladium cuspidatum*, *A. cordifolium*, *Mnium affine* s.l. and *Aneura pinguis*.

In respect of flower colour, the plants of *D. incarnata* in this region fall into three classes, as at Redgrave Fen, viz., flesh pink, purple and yellowish white. As is not the case at Redgrave Fen, however, a further classification into morphological forms is possible, a classification which may be based, in the first instance, simply upon labellum size. A group with small labella corresponds in general facies to subsp. *incarnata*, and another, in which the labellum is considerably larger, is here referred to subsp. *gemmana*.

The representation of these flower colour and labellum size groups in a sample of 170 plants from Sutton Broad is given in Table VIII. In this locality, all of the plants with purple flower colour fall in the group with larger labella.

TABLE VIII.—Distribution of flower colour and labellum size classes in a sample of 170 plants from the colony M4, Sutton Broad, Norfolk.

	Yellow-white (*c.* Séguy 270)	Purple (Séguy 59)	Flesh pink (Séguy 18–19)
subsp. *incarnata*	25	—	56
subsp. *gemmana*	—	21	68

The distribution in respect to labellum shape and patterning is shown in Table IX. All groups show agreement in labellum shape. The two colour classes under subsp. *gemmana*, whilst agreeing between themselves in the dominance of pattern grade 2, differ from the group with anthocyanin pigmentation under subsp. *incarnata*, in which the characteristic patterning of the subspecies, grade 3, prevails. Again, those plants without anthocyanin pigmentation necessarily bear concolorous labella.

The considerable difference in the dimensions of the floral parts is apparent from the sample data given in Table X (see also fig. 13). Again there is agreement between the two colour forms in each size class ; the latter, in respect to range of labellum size, do not overlap at all.

The Sutton Broad colony thus consists of two morphologically distinct classes. One, corresponding to subsp. *incarnata* in flower size and labellum shape, contains approximately two thirds of individuals agreeing with that subspecies in flower colour and patterning, and one third which match in flower colour (but not in labellum shape) subsp. *ochroleuca*. The other morphological group consists of individuals larger in all floral dimensions, carrying a concolorous labellum or one marked lightly with a pattern of dots, and exists in two colour forms, a flesh pink (matching subsp. *incarnata*) and a magenta (matching rather *D. praetermissa* than *D. incarnata* subsp. *pulchella*). Vegetative data for the sample from this second group are recorded in Table XII. In mean stature, this sample is exceeded only by O1, of subsp. *ochroleuca* ; in other characteristics it is evidently unique. The high average leaf number, more than 6, is particularly notable.

TABLE IX.—Labellum pattern and shape distributions (scored in grades corresponding to those of figs. 1 and 2) in a sample of *D. incarnata* from colony M3, Sutton Broad, Norfolk.

Class	Pattern grades				Shape grades				
	1	2	3	4	1	2	3	4	5
subsp. *incarnata* :									
flesh pink	—	—	51	5	—	1	24	25	6
yellow-white	25	—	—	—	—	3	7	13	2
subsp. *gemmana* :									
purple	—	21	—	—	—	—	8	13	—
flesh pink	—	68	—	—	—	—	28	37	3

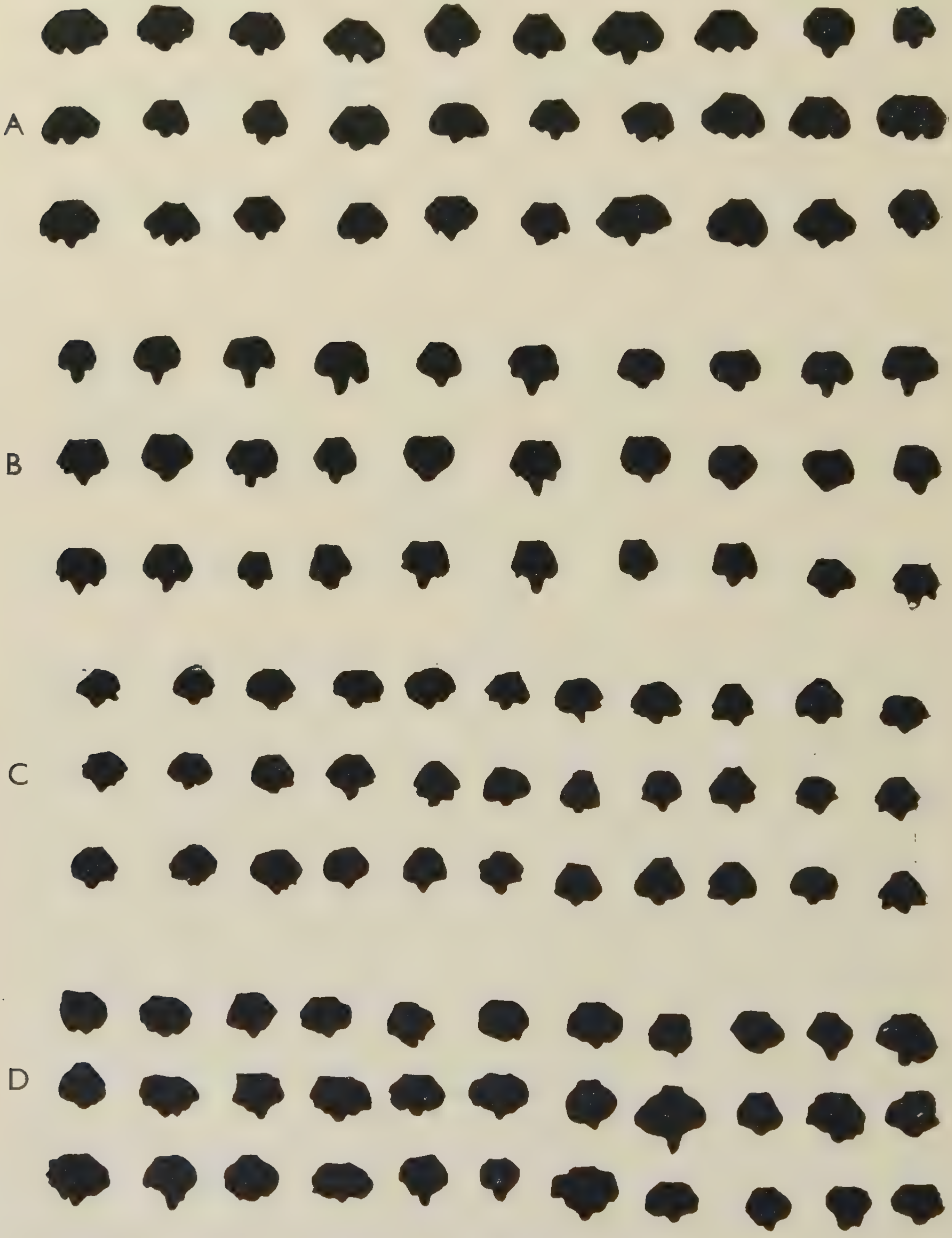

Fig. 11.—Silhouettes of labella from population samples of D, *D. incarnata* subsp. *pulchella*. A, P7 (Borth Bog); B, P11 (Lough Mullaghderg); C, P1 (Hartland Bog). All ×*c*. 1.

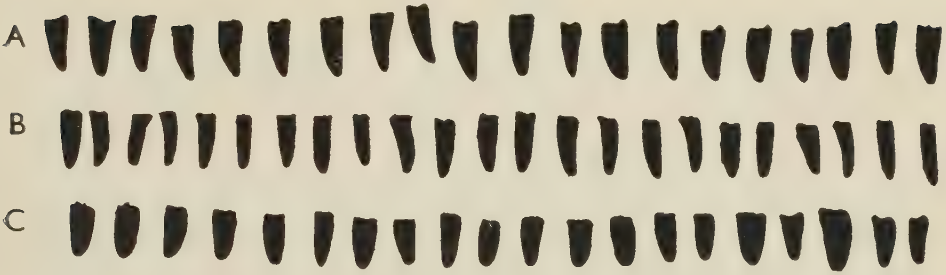

FIG. 12.—Silhouettes of spurs from labella of *D. incarnata*. A, P7 (Borth Bog); B, P11 (Lough Mullaghderg); C, P1 (Hartland Bog). All ×*c*. 1.

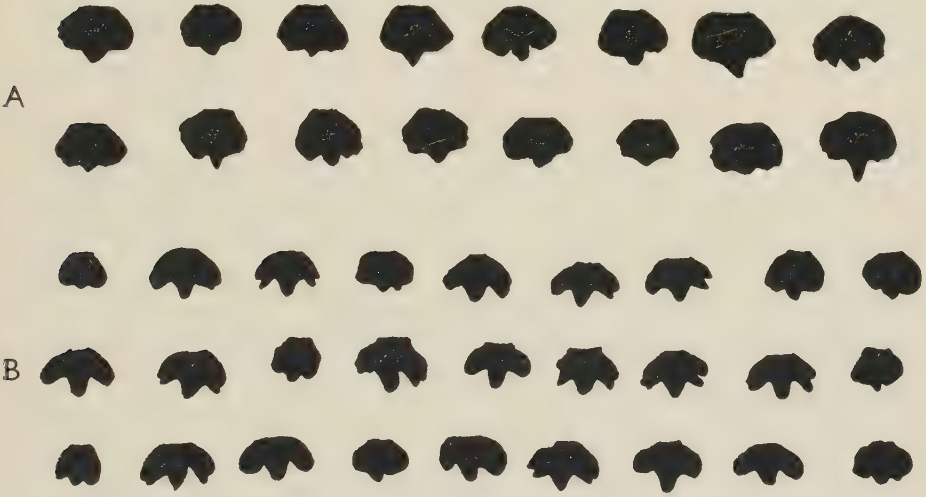

FIG. 13.—Silhouettes of labella from population samples of *D. incarnata*. A, subsp. *gemmana* (Sutton Broad); B, subsp. *ochroleuca* (Blo Norton Fen). All ×*c*. 1.

Plants of a similar type have been encountered in various parts of East Anglia, mostly in numbers too small to justify biometrical study. They are distinguished by the tall, robust leafy habit, long inflorescences of large flowers and large bracts. Pugsley's brief diagnosis of subsp. *gemmana* (as var. *Gemmana* of *Orchis latifolia*) details no floral differentiae, but emphasizes the vegetative robustness, and it is because of the agreement of these East Anglian plants in this characteristic that they are placed under subsp. *gemmana*.

TABLE X.—Labellum and spur dimensions in a sample of *D. incarnata* from colony M3, Sutton Broad, Norfolk.

Class	Labellum		Spur	
	Length (mm.)	Width (mm.)	Length (mm.)	Width (mm.)
subsp. *incarnata*:				
flesh pink	5·99±0·07	6·57±0·09	7·50±0·08	2·70±0·04
yellow-white	5·70±0·09	6·47±0·15	7·50±0·10	2·80±0·06
subsp. *gemmana*:				
purple	8·09±0·13	10·11±0·23	8·60±0·16	3·43±0·07
flesh pink	7·70±0·16	9·72±0·15	8·42±0·07	3·52±0·06

TABLE XI.—Dimensions of vegetative parts in a sample of 50 plants of subsp. *gemmana* from colony M3, Sutton Broad, Norfolk.

Stature (cm.)	Leaf number	Leaf length (cm.)	Leaf width (cm.)
44·9±1·27	6·06±0·08	17·19±0·34	2·34±0·06

The difference in vegetative robustness from other British forms of *D. incarnata* is indeed so remarkable that some doubts were entertained about the status of this form within the species. Some individuals approaching 1 m. in height in which the labellum was scarcely reflexed laterally were reminiscent rather of the southern European *D. sesquipedalis*. Cytological investigation of several plants from Sutton Broad has, however, revealed a uniform chromosome number of $2n=40$, and there can be little doubt that the subspecies is rightly placed among the *Incarnatae*.

REPRODUCTIVE BIOLOGY.

The probable function of the floral mechanism of the dactylorchids as a device to preclude geitonogamy has been recognized since the investigations of Darwin (1862) and Müller (1883). Nevertheless, Martens (1926) has suggested that autogamy may occur in one dactylorchid species, *D. maculata*, and clearly were it also habitual in *D. incarnata* some of the above facts would appear in a different light. Compatibility and the possibility of autonomous self-pollination have been investigated in plants in cultivation during the seasons of 1950, 1952 and 1953. Plants tested were from the following sources: 1950, subsp. *pulchella*, Co. Down; subsp. *coccinea*, Co. Donegal; 1952, subsp. *incarnata*, Hampshire; subsp. *pulchella*, Dorset and Hampshire; 1953, subsp. *incarnata*, Norfolk and Hampshire; subspp. *pulchella* and *ochroleuca*, Norfolk. All were transplanted from the wild in bud or early flower during the season of testing, and all previously opened flowers were excised. After three or four days' isolation, the following treatments were given in each inflorescence to flowers at the same stage of opening: (*a*) pollinia withdrawn from the thecae and placed directly upon the stigmata of the same flower; (*b*) pollinia withdrawn and destroyed, and the stigmata heavily pollinated from two or more plants originating in the same natural population; (*c*) pollinia withdrawn, and the flowers left unpollinated; and (*d*) pollinia left in place with no natural or artificial disturbance of the flower.

Flowers receiving treatments (*a*) and (*b*) showed signs of the effect of pollination in all cases within five or six days, the tepals losing turgidity and darkening. Swelling and untwisting of the ovary followed in 1–2 weeks. No difference was discernible in the seed-output of cross- and self-pollinated ovaries on the same plant in any of the forms tested.

Unpollinated flowers (treatments (*c*) and (*d*)) lost turgidity less rapidly than those which had been pollinated, and the tepals untimately faded without marked swelling of the ovary. In flowers from which pollinia were not removed (treatment (*d*)) their spontaneous release from the thecae was never observed; there is thus no evidence of the occurrence of autonomous self-pollination.

It therefore appears that the various forms of *D. incarnata*, although self-compatible, are in fact mechanically incapable of autogamy and are guarded against geitonogamy by various floral adaptations; they must be considered practically obligate outbreeders.

At the same time as the above tests, preliminary observations were made upon the interfertility of the various forms, based upon seed-set following artificial cross-pollination. Seed-set was normal in all of the following combinations (asterisk indicates where reciprocal tests were made): * subsp. *incarnata*

× subsp. *pulchella* ; * subsp. *incarnata* × *ochroleuca* ; subsp. *incarnata* (f) × subsp. *gemmana* ; subsp. *incarnata* (f) × *coccinea* ; subsp. *pulchella* (f) × *ochroleuca* ; subsp. *pulchella* (f) × subsp. *coccinea*.

The cytological results of the above experiments will be published in detail elsewhere.

Phenology.

Among the more strongly differentiated populations of *D. incarnata* there are differences in flowering-time of a magnitude sufficient to suggest that this may act as a reproductively isolating factor.

In Hampshire and Dorset, polymorphic colonies of the species are uncommon, and the populations mostly fall into two groups corresponding to the subspp. *incarnata* and *pulchella*. Observations during 1951, 1952 and 1953 suggest that, at comparable latitudes, flowering in populations of subsp. *incarnata* attains a peak some 10–15 days earlier than in those of subsp. *pulchella*. There is nevertheless a considerable overlap, since flowering commences in subsp. *incarnata* in mid-May and continues into late June, subsp. *pulchella* beginning in late May and continuing through June even into July.

The correlations are less clear in East Anglia. Here the subsp. *incarnata* flowering period seems more or less the same as in Hampshire and Dorset, and subsp. *ochroleuca* is practically coincident. The flowering period of the Walton Common population referred above to subsp. *pulchella* is 7–10 days later, again with a considerable overlap, but in most of the polymorphic colonies there is little evidence to suggest flowering time differences between the various forms present. A striking exception is that around Sutton Broad (see M4 above). The segment of this referred to subsp. *gemmana* reaches a flowering peak some 10 days later than the subsp. *incarnata* component, although there is an overlap of at least two weeks.

Such evidence as is available suggests that Scottish and western Irish populations of subsp. *incarnata* flower on the average a week or a fortnight later than those of southern England. Those of subsp. *pulchella* in the north and west are, however, remarkably variable. Colonies in the calcareous fens of west-central Ireland are relatively early flowering, reaching a peak in mid-June. Those of mildly acid *Sphagnum* bog in the same area are later by up to a fortnight, and among thinly scattered populations on Mayo blanket bog individuals have been encountered in flower in August. Similar late-flowering populations exist in Scottish bogs.

A latitudinal variation is apparent in the flowering time of subsp. *coccinea*. Southern English populations attain a peak a week to a fortnight later than *incarnata* at the same latitude, but there is less difference in time of onset of the main flowering period along the western Irish seaboard. Further north, in the Hebrides, some colonies of subsp. *coccinea* show a protracted flowering period, extending from mid-June into early August.

DISCUSSION.

The foregoing analysis of some characteristic populations will have made clear the main features of the variation pattern of *D. incarnata* in the British Isles, as well as illustrating the point made in the introduction, that the taxonomic subdivision into subspecies is of limited applicability. The named subspecies represent specialized ' radiations ' of the species, all of which are not of the same degree of homogeneity ; in addition there is a residue of heterogeneous populations which cannot be referred, as populations, to any one infraspecific taxon. It is not the intention in this paper to attempt any general interpretation or explanation of this variation pattern : fuller understanding must await further information, particularly about such matters as the behaviour of pollen vectors in relation to the various flower patterns and colours. In any case, a satisfactory interpretation can hardly be based upon observations limited to the British Isles, a small sector indeed of the range of the species. The species is variable throughout its Eurasian range, and there is some evidence that the differentiation of ecological races may, in some regions, be more complete. Were this so, the complications in the British Isles would signify little enough, and could probably be interpreted simply as the outcome of race admixture and consequent introgression following centuries of continuous human modification of habitats. This certainly appears a very probable explanation for the situation in East Anglia, where in the last four or five centuries such drastic changes in the area and nature of habitats available for fen and marsh species have taken place. It is at least suggestive that the populations of the more uniform facies in the British Isles are mostly to be found in the more stable, less disturbed—and in this sense, more ' natural ' —habitats.

Among the very large number of infraspecific taxa which have been described on the Continent under *D. incarnata* (von Soó, 1930–40, lists some 37, and Vermeulen, 1949, has recently added several others), there are some with such obvious affinities with British forms that discussion of them is desirable here.

Subsp. *incarnata.* The British plants here placed under this subspecies correspond to what is widely accepted as the ' type ' of the species by Continental monographers (Ascherson & Graebner, 1097 ; E. G. & A. Camus, 1928–9 ; von Soó, 1930–40 ; Vermeulen, 1947, and others). It is probably the most wide-ranging of all dactylorchid taxa, since populations corresponding in floral characteristics occur throughout the entire range of *D. incarnata*, including all of western and central Europe, and probably extending eastwards in Russia as far as Lake Baikal (Klinge, 1898 ; Nevski, 1935).

Subsp. *ochroleuca.* In the British Isles, this subspecies is known with certainty only from East Anglia. The Continental distribution has recently been treated by Nannfeldt (1944), who emphasizes the distinction of the typical form of the subspecies, characterized by ochroleucous flowers and a distinctly three-lobed labellum, from albino or pale-flowered forms occasionally to be found in populations of the type and other subspecies. In Sweden, the plant is " restricted to the most calcareous parts of the provinces of Scania, Oland, Gotland, Ostergotland and Vastergotland, where it inhabits only extreme rich fens ", and Nannfeldt produces evidence that it occurs exclusively in this type of habitat elsewhere in Europe. Perhaps because of this habitat limitation, populations of typical *ochroleuca* facies are much more uncommon than those of subsp. *incarnata*, but nevertheless the European distribution is a wide one, including Scandinavia, north to 62° N. latitude, the Baltic countries ; north and central Germany extending possibly into France ; the Alps and associated mountain systems (Gsell, 1935). The eastern limits are uncertain.

Subsp. *coccinea.* Almost all of the populations of *D. incarnata* inhabiting dune slacks in coastal districts of the British Isles are referable to this subspecies, and in Ireland, colonies of similar facies occur in inland districts, usually in relatively dry meadows or pasture-land, but sometimes on lake shores. Similar forms undoubtedly occur in coastal sand dunes in other countries of western Europe, but they appear to have attracted little taxonomic attention. Vermeulen records his var. *dunensis* (which is based upon Druce's *incarnata* var. *dunensis*, a plant probably assignable to subsp. *coccinea* ; Pugsley, 1935) as occurring in the Netherlands. Forms similar in habit (var. *seemenii* Asch. & Graebn. and var. *obscura* Höppner, both associated with *D. purpurella* by von Soó, 1930–40) and colour (lus. *rubriflorus* Harz) are catalogued by other Continental monographers, but in no case is a sand dune habitat specifically indicated.

Subsp. *gemmana.* Plants conforming with this subspecies as it is interpreted above occur in scattered fen habitats in southern and eastern England, and in one or two similar localities in western Ireland. Several Continental varieties and forms of *D. incarnata* have been based upon vegetative robustness. Among these are *Orchis incarnata* var. *subfoliosus* Schultze apud Asch. & Graebn. var. *macrophylla* Schur. and var. *latissima* Zapal. The latter, transferred by Vermeulen (1949) to *Dactylorchis incarnata*, is said by that author to be "synonymous for the greater part with *Orchis latifolia* var. *gemmana* Pugs.". Labellum size is not adopted as a diagnostic in any of the descriptions of these taxa, although it is certainly a striking feature of plants placed under subsp. *gemmana* above. In all, it would seem premature to attempt to homologize any of the infraspecific taxa distinguished by Continental workers with subsp. *gemmana* as interpreted here.

Subspp. *pulchella* and *cruenta*. In the arrangement here adopted, it has been considered most expedient to group all of the British purple-flowered colonies under subsp. *pulchella*, and the few Irish ones in which leaf marking is prevalent under subsp. *cruenta*, recognizing, of course, that there is intergradation. Subsp. *cruenta* in Ireland is restricted to highly calcareous fens, a habitat in which similar forms occur in Scandinavia and the Central European mountains (detailed distribution given in Heslop-Harrison, 1950). Subsp. *pulchella*, as demonstrated above, shows some degree of internal ecoclinal differentiation along a habitat sequence ranging from calcareous *Schoenus* marsh to acid *Sphagnum* bog. The southern English forms, including those of the original type area, the New Forest, lie for the most part at the fen end of this sequence ; in Scotland and Ireland, colonies of a similar facies occur in corresponding habitats, but most of those in the north and west of the British Isles in areas not subject to the influence of calcareous ground-water fall towards the other end. In addition, subsp. *pulchella* in the broad sense adopted here embraces many populations with purely local character combinations which do not fall on the ecocline.

Many varieties and forms have been named by Continental authors which appear to have affinities with subsp. *pulchella*. Discounting those which refer to colour forms with unspecified distributions (lus. *purpurea* Hoppner, lus. *pulcherrima* Holzfuss, etc.), two in particular are of interest. The earlier, *Orchis incarnata* var. *serotina*, appears in Max Schultze's monograph of the German Orchidaceae (1894) and is attributed to Haussknecht, who had not apparently previously published a description. This variety is said by Schultze to occur in *Sphagnum* bog, and is referred to by von Soó as a characteristic ecotype of heather moor. The description defines a form similar to those occurring at the acid-soil end of the ecocline in the British Isles, and there can hardly be any doubt that var. *serotina* marks the same end of a corresponding sequence of forms on the Continent. It may be noted that in von Soó's subdivision of *Orchis incarnata* (1930–40), Druce's var. *pulchella* is placed as a questionable form *under* var. *serotina* Hausskn. ap. Schultze, em. Soó.

The second plant of interest is Neuman's *Orchis incarnata* var. *borealis* (1909). The description of this plant certainly defines a form which would fall within the ambit of subsp. *pulchella*. The bulk of *D. incarnata* populations in Scandinavia appear to conform to var. *borealis*, and intergradation with subsp. *cruenta* is again apparent. There can be little doubt that an analysis of purple-magenta flowered populations of *D. incarnata* in Scandinavia would reveal a pattern not unlike that in the British Isles. There is, however, no indication of the existence in the northern part of the range of the species of races inhabiting acid moorland or bog habitats.

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A CONSIDERATION OF FRESHWATER ALGAE OF SIERRA LEONE

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Existing records of algae, freshwater and brackish, for Sierra Leone are confined to a few collections made over 50 years ago from its coastal districts and examined by European algologists, commencing with a brief note by O'Meara (1876) concerning the identity of a *Coscinodiscus* in the Rokel River. A further collection from the same river, of which an alternative name is the R. Seli under which it appears in the present survey, was examined by the diatomist A. Grunow who published the original diagnoses of these tropical West African forms in the well-known treatise, Cleve & Grunow's "Arctic Diatoms" (1880) ! In 1898 Leuduger-Fortmorel considered that the freshwater diatoms of West Africa would probably be similar to those already described from other parts of the world, and his analysis of material obtained from the lower reaches of the Great Scarcies River bore out his statement ; these records may easily be overlooked owing to the misleading title of the paper. His collection from Mambolo, a small 'port', is now of especial interest, for the Rice Research Station has been established at Rokupr, a few miles upstream ; extensive collections are being made there for the purposes of this survey of Sierra Leone algae.

Excluding these meagre diatom contributions to the literature, the sum total of algae known for Sierra Leone in 1950 was less than a score of species, most of which are brackish-water organisms. W. & G. S. West found 4 blue-green species in Dr. Welwitsch's Collection, obtained from Freetown ; their occurrence is hidden in the Angola paper (1897). Little has been published, too, for the neighbouring states of Liberia (seven diatoms and a desmid) or French West Africa (A.O.F.) where Zanon's study of collections made by Scaetta and Capra yielded 360 diatoms for the whole range of those French colonies. Material from the hinterland of West Africa has almost been unavailable, so that the opportunity to examine an extensive series of samples made from the Sula Hills in the north of the Protectorate of Sierra Leone has enabled us to supply a little knowledge about an unknown algological territory.

This collection was made during the period 1950–1952 by the late W. N. Woodhead, whilst engaged on geological survey duties traversing these Hills, starting in the Tonkolili District and working north-eastwards to the swampy Lake Sonfon. It amounted to 64 tubes in all. The area is drained by two major river systems, the Seli or Rokel, and the Pampana, which in turn is a tributary of the Jong River. The Sula Hills range from 1000 ft. to nearly 5000 ft. and continue the high ground of French Guinea. The samples were taken from a wide variety of ecological situations, from the swamps and rivers, rice-fields and pools, etc., during both the wet and dry seasons of the year. They have yielded an extensive flora, outnumbering in taxa any published data yet available from the continent of Africa ; our later surveys, which are still in progress, of material from many other parts of the Colony and Protectorate, indicate that the algal flora of the Sula Hills is but the fringe of an exceptionally rich assemblage. In this present contribution we enumerate 430 species in addition to taxa of more subordinate rank. They are distributed :—

	Species	Varieties, etc.	Taxa new in Africa	Taxa new to science
CHLOROPHYTA :				
Volvocales	7	—	—	
Chlorococcales	11	—	3	—
Ulotrichales	5	—	—	—
Chaetophorales	1	—	—	1
Oedogoniales	4	—	3	—
Zygnematales	152	42	35	30
CHRYSOPHYTA :				
Xanthophyceae	5	—	4	—
Chrysophyceae	3	—	—	2
Bacillariophyceae	177	68	55	21
PYRROPHYTA	2	—	1	—
EUGLENOPHYTA	20	2	10	3
Protomastigineae	1	—	1	—
RHODOPHYTA	1	—	—	—
CYANOPHYTA	41	—	10	5
Totals	430	112	122	62

Our anticipation of a rich Myxophycean flora and a probable heavy population of diatoms was not fully realized ; though the diatoms are present in enormous quantities as well as being representative of numerous species, the blue-green algae are scanty. On the other hand there is an extraordinary profusion of desmids and filamentous Conjugatae in many of the localities.

The scarcity of other Chlorophyta may be due to the lack of plankton material, though it is significant that few are reported from the lists compiled for Central Africa, e.g. G. S. West, 1907.

The richest gatherings were made at Lake Sonfon where many unusual species of diatoms and desmids were equally represented ; other good results were found in samples from the rivers Chigara and Kangofurina, from rice-fields near Sunkoni and from pools on the high ground near Gerinka.

DIATOMACEAE

Though the commonest diatoms are cosmopolitan species (e.g. *Synedra ulna* (Nitzsch) Ehr., *Eunotia curvata* (Ktz.) Lagerst., *Vanheurckia rhomboides* (Ehr.) Bréb.) there exist (i) a small selection usually considered as northern in their distribution (e.g. *Coscinodiscus lacustris* Grun. in Cleve & Grun. var. *septentrionalis* (Grun.) Rattray, *Achnanthes flexella* (Bréb. ex Kütz.) Brun var. *alpestris* Brun and *Eunotia Nymanniana* Grun., and (ii) diatoms restricted to the tropics (e.g. *Synedra dorsiventralis* O. Müll., *Eunotia monodon* (Ehr.) Ehr. var. *tropica* (Hust.) Hust., which is common in the Sula Hills, and *Cymbella javanica* Hust.). *Melosira, Cyclotella, Rhopalodia, Epithemia* and *Surirella* species are scarce. *Diatoma* and *Tabellaria* are almost absent, whilst *Fragilaria* takes only a modest place : on the other hand *Eunotia, Navicula, Pinnularia* and *Gomphonema* are prolific.

Zanon (1938) described from Kivu, Belgian Congo, a rod-shaped diatom with truncate capitate poles sharply abstricted from the rest of the frustule as *Synedra strangulata*. Later, Hustedt (1949) found in the Albert National Park diatoms similar in shape and size, but demonstrated a faint pseudoraphe and distinct marginal teeth ; he regarded them to be the same as Zanon's plants and transferred them to *Fragilaria* as *F. strangulata* (Zanon) Hust. Numerous specimens of comparable diatoms were found by us in a Maranda gathering. Realgar or arsenic selenide mounts reveal the teeth as obtuse knobs set a little distance away from the frustule margin so that they are difficult to resolve when a frustule is viewed from directly above. The teeth are most conspicuous in the girdle view, which is remarkably deep. *F. strangulata* occurs elsewhere in Sierra Leone and may well prove to have a wide distribution in West Africa.

Tooth-like projections occur also in *Eunotia* into which genus Hustedt (1949) placed species of *Desmogonium* : both *E. lineolata* Hust. (= *Desmogonium guyanense* Ehr. in Schomberg) and *E. rabenhorstianum* (Grun.) Hust. occur in Sierra Leone, the former appearing in abundance in the samples taken around Lake Sonfon.

Actinella pliocenica Hérib. & Perag. in Hérib., in which the upper pole is markedly acute, has been found in Lake Sonfon, R. Kangofurina, etc. Previously this *Actinella* was known only as a fossil in Auvergne whence it was originally described and illustrated from a fragmented specimen. Our material includes numerous complete specimens which permit a record of dimensions to be added to the original diagnosis (length 102–120 μ, upper swelling 6·5–10·2 μ wide, the the stem 3 μ wide). *Actinella* had not been reported from Africa before but other species of this unusual genus have now been detected in West African gatherings and will be considered in a separate contribution. *Amphicampa hemicyclus* (Ehr.) Karsten in Engler was found in a pool at Maranda and in the Tonkolili ; these seem to be the first notices of this distinctive diatom in Africa. *Asterionella fibula* (Bréb.) Hust. was found in a stream at Sunkoni in stellate groups. This diatom has long been known as *Peronia erinacea* Bréb. & Arnott, but was recently shown by Hustedt (1952) to be a stellate *Asterionella*.

The material yields a tropical locality for *Navicula bryophila* Petersen in a Tonkolili gathering. It has been recorded for Indonesia, Moçambique and Tunisia though it is more widely regarded as an aerophilous diatom in north temperate regions. It may be profitable to re-examine tropical records of *N. subtilissima* Cleve, which has a close similarity with *N. bryophila*. *N. hambergii* Hust. occurs in a stream at Sunkoni; this is presumably the first African notice of a species that may well be cosmopolitan as it has been seen in Europe, North America and Indonesia.

Though *Surirella bifrons* (Ehr.) Ehr. is extremely rare in the Sula Hills, **S. bifrons** var. **heteropolis** (Hust.), comb. nov., appeared frequently in the R. Kangofurina. Hustedt described this distinctive variety (in *Int. Rev. Hydrobiol.*, **42,** 146 (1942)) as *S. biseriata* var. *heteropolis* from Celebes. *Stenopterobia delicatissima* (Lewis) Van Heurck occurs in abundance in a few places, and *S. intermedia* (Lewis) Van Heurck was found in Lake Sonfon, the first record for Africa.

CONJUGATAE.

Filamentous Zygnemataceae are common in most places but very few species have been named because of the absence of zygospores; a similar embarrassment is encountered with the Oedogoniaceae and Nostocaceae. The wealth of desmids is extraordinary; many of the taxa enumerated are limited to the tropics with a pronounced similarity with those known for Brazil.

A form of *Phymatodocis irregulare* Schmidle was found in a sporing condition in Lake Sonfon; vegetative filaments had been recorded for Transvaal and Tanganyika in Africa, and the species is known to be present in the Amazon basin, Ceylon, Burma and Java. Ripe zygospores had, however, never been described. They are rectangular with strong concavities at the corners when seen in front view. They are large, occupying all the space between the conjugating filaments and most of the cell width as well. Other filamentous desmids such as *Hyalotheca* and *Bambusina*, have only occurred in rare degree. Three species of *Desmidium* have been found, mainly in the R. Singin, *D. baileyi* (Ralfs) Nordst. presumably for the first time in continental Africa though it had been reported for Madagascar. *Triploceros* also has not appeared in lists of African desmids, but numerous empty semicells of varieties of *T. gracile* Bailey appear in the same material as that in which *Phymatodocis* was found. This genus is not confined to the tropics, for there are well-known localities for it on the mainland of Canada, and we have found it in material from Newfoundland. Our African specimens make a noteworthy extension to the range of this characteristic species. Amongst these rare forms also appears a small amount of an *Ichthyocercus*, which cannot, however, be reconciled with *I. angolensis* W. & G. S. West, described from Dr. Welwitch's Angola material (1897).

Cosmarium and *Closterium* with 65 and 24 species respectively, *Euastrum* and *Micrasterias* with 13 and 5 species in the Sula Hills are usually present in quantity of individuals in most of the samples. Elsewhere in Sierra Leone *Micrasterias* becomes even more prominent. *M. ceylanica* Fritsch has been observed for the first time in Africa. Most of the *Euastrum* and *Closterium* species found are those with wide geographical ranges, but *E. platycerum* Reinsch had hitherto been reported only from Europe. *Cosmarium pseudobroomei* Wolle is easily the commonest desmid in these samples whilst *C. retusiforme* (Wille) Gutw. is also abundant in a few widely scattered places. Few of the north temperate *Cosmarium* species observed attain ecological prominence; *C. punctulatum* Bréb., *C. pyramidatum* Bréb. ex Ralfs and *C. tinctum* Ralfs, for instance, have only been traced now and then, each in a single sample. *Cosmarium* species with heavily ornamented membranes are freely observed. *C. tessalatum* (Delp.) Nordst. has occurred once at Maranda in the Sula Hills, but proves to be quite common elsewhere in the Protectorate. *C. decoratum* W. & G. S. West has a wide distribution in Sierra Leone; it was erected on Malagasy material and has been recorded for Transvaal so that it may possibly have a wide distribution in Africa.

Staurastum is weakly represented, the commonest species being *S. telijerum* Ralfs, which had not previously been reported in African material, though it appears in the Azores. It has been traced in a wide variety of habitats but seems to avoid Lake Sonfon. van Oye (1943) stated that his identification of *S. margaritaceum* Ralfs from the Albert National Park was the first time it had been found in African collections since de Wildeman had recorded it at the turn of the century ; we have found it now in the R. Chigara, but it still seems that it is very rare in African waters in contrast to its frequent occurrence in Europe. The distribution of *S. quadricornutum* Roy & Biss. has been extended to Africa now that we have found it at Maranda ; it had been recorded for Japan, Indonesia and the U.S.A. previously. *Arthrodesmus* is absent. Three species of *Xanthidium* have been noted, including *X. raciborskii* Gutw. which Krieger (1932) had previously recorded from the tropics (Indonesia).

BLUE-GREEN ALGAE.

Very few Chroococcaceae appear, and those species that have been listed are rare in quantity. The filamentous genera are also few in number, but some have appeared in a limited abundance, *Anabaena* species in particular. *Oscillatoria tenuis* Gom. occurred in several places freely, but is quite lacking in the Lake Sonfon area. A beautiful *Petalonema involvens* (A. Br.) Migula has been seen in several collections around the settlement of Gbulia. *Cylindrospermum* is represented only by *C. alatosporum* Fritsch, gathered in three places around Gbulia, but this sparseness is in contrast with its abundance and ecological importance in Sierra Leone as a whole.

OTHER ALGAE.

Lake Sonfon proved to be good for Euglenineae, particularly *Trachelomonas*, but those species considered ' common ' in Europe or North America [e.g. *Euglena viridis* (Schrank) Ehr. or *Trachelomonas volvocina* Ehr. do not occur in quantity. Interesting additions to African lists are *Euglena spirogyra* Ehr. var. *suprema* Skuja, *Phacus acuminata* Stokes, *P. undulata* (Skv.) Poch., *Trachelomonas sydneyensis* Playf. and *T. superba* Swir.

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STUDIES OF THE DECOMPOSITION OF SEAWEEDS AND SEAWEED PRODUCTS BY MICRO-ORGANISMS

By C. G. C. Chesters, A. Apinis and M. Turner.

Introduction.

Decomposition of cast seaweeds results from the autolysis of moribund protoplasts, from the ingestion and digestion of thalli by diverse animals, including larval stages of flies, and from the growth of a complex series of micro-organisms which in total constitute an ecological association possessing many interesting and potentially valuable characteristics. In the main, this association consists of bacteria, actinomycetes and microfungi, and the present communication is concerned with certain of these which are demonstrated to attack particular constituents of the thalli of brown seaweeds.

When investigating a complex population of micro-organisms it is often difficult to disentangle the several individuals and to demonstrate the exact part which each plays in any series of decomposition stages. Therefore, this initial investigation was limited to an examination of these organisms which could be shown to attack and decompose sodium and calcium salts of alginic acid, and laminarin. The first stage of the investigation aimed at the demonstration of the production by micro-organisms of enzymes which could attack these particular compounds, and the second at the isolation of cell free extracts of these enzymes.

Previous Investigations.

Alginic acid, or mixed salts of this acid, constitute some 10 to 40 per cent of the dry weight of brown algae. The acid is a long chain polymer of D-mannuronic acid. An alginase, capable of reducing the viscosity of a solution of alginic acid at pH 7·2, was isolated by Yukiyoshi (1931) from the intestines of *Haliotus giganteus* and was obtained as a solid of high activity. Allen (1934) demonstrated that bacteria isolated from soil were capable of hydrolysing alginic acid and Waksman, Carey & Allen (1934) considered this property was seldom characteristic of fungi. Bacteria isolated from sea-water, from marine plankton, from mud deposits of the sea floor, and from soils were shown to be capable of decomposing alginic acid in the free state and in combination in weed thalli. While active enzyme preparations could be obtained from such bacteria, fungi capable of attacking cellulose and hemicellulose were able to decompose alginic acid only to a limited extent. Waksman & Allen (1934) found that the alginase isolated from bacteria reached optimum activity at pH 7·0 in solutions containing 2·0 per cent NaCl and at a temperature of 40° C. Of the four active bacteria which they isolated, three were obtained from sea-water and one from soil. Waksman and his co-workers considered these organisms to be new species, and proposed names for them, but did not fully describe their characteristics. Thjøtta & Kass (1945) demonstrated that 12 out of 200 strains of bacteria isolated from sea-water reduced the viscosity of alginic acid whereas 9 out of 200 strains isolated from soil possessed this property. Kass, Lid & Molland (1945) considered that the ability to decompose alginic acid could be used as a determinative character for bacteria belonging to the *Pseudomonadeae* and the *Eschericheae*.

Laminarin can be isolated from brown algae as water soluble and water insoluble forms and consists of β-D-glycopyranose units combined in a 1-3 linkage. Barry (1941) isolated a laminarinase from the crop and stomach of the edible snail and Dillon & O'Colla (1950 and 1951) demonstrated a similar enzyme in oats, barley, potato and hyacinth. Dillon & O'Tuama (1935) found that wheat β-amylase could hydrolyse laminarin. Micro-organisms have not yet been reported to produce a laminarinase.

Since there have been no previous records of laminarin hydrolysis by micro-organisms most of the experimental work reported here concerns the demonstration of laminarin decomposition by selected strains of bacteria and actinomycetes, the examination of the influence of certain factors on the production of laminarinase, and the isolation of an active cell free extract. Alginase activity by bacteria has already been reported and the present work confirms this and demonstrates that alginase is also produced by strains of actinomycetes.

ISOLATION PROCEDURES.

Micro-organisms capable of decomposing alginates and laminarin were isolated from the decaying thalli of species of brown algae, from decaying masses of cast seaweeds, from lagoon muds containing the remains of seaweed thalli, and from salt marsh soil and sand. Elective methods of isolation were used in which the decayed material was added to a mixture of sterile *Ascophyllum nodosum* meal with sand and incubated at 20° C. for varying periods, and in which the collected material was mixed with sterile sand and exposed to a continuously percolating stream of alginate or laminarin (Audus, 1946). Active organisms were isolated from suspensions in normal saline prepared from the incubated *Ascophyllum* meal, or from the percolate and the seaweed–sand mixture. The isolation medium consisted of 2·0 per cent agar containing the minerals of a Czapek-Dox medium plus 0·1 per cent Bacto yeast extract and either 1·0 per cent calcium alginate or 2·0 per cent insoluble laminarin as the sole carbohydrate source. The medium was adjusted to pH 7·0 and in one series during each experiment 2·0 per cent of sodium chloride was added. Calcium alginate remains as a finely divided precipitate during sterilization and in the cooled and set agar; insoluble laminarin dissolves completely during sterilization but is precipitated as the agar cools to form an evenly opaque medium. Plates seeded with dilutions from the elective cultures and incubated at 25° C. produced a wide variety of fungal, actinomycete and bacterial colonies. Those species capable of hydrolysing the alginate or the laminarin could be discerned with ease by the hyaline zone surrounding the colony and sharply defined against the opaque medium. Such active colonies were often mixtures of two or more species whose separation was effected by routine dilution techniques. Frequently only one of the associated organisms was responsible for the hydrolysis of the carbohydrate source. Stock cultures were maintained on Czapek-Dox alginate or laminarin media, and on standard bacteriological (nutrient agar) and fungal (potato-dextrose agar) media. Very active organisms sometimes became attenuated when grown on stock media and even on media containing either alginate or laminarin. Some species completely lost their activity after prolonged cultivation in the laboratory. Repeated isolations have demonstrated that alginate and laminarin hydrolysing bacteria and actinomycetes can be obtained at will from suitable natural substrates when elective methods of isolation are employed.

ORGANISMS ISOLATED.

Bacteria and actinomycetes are the most active alginate and laminarin decomposing organisms. While certain fungi were demonstrated to hydrolyse laminarin the rate of hydrolysis was slow. From the total number of initial isolations prepared, about 53 strains of bacteria and 17 strains of actinomycetes decomposed alginates or laminarin or both. Although precise identification is not yet completed the number of individual species involved is limited. Many of the species cannot be definitely assigned to already described species with any degree of certainty. Of these strains only a few were responsible for really active decomposition of the specific substrates. Table I summarizes the sources of cultures and indicates the numbers of strains which gave clearly positive reactions.

TABLE I.—Distribution of strains of bacteria and actinomycetes capable of hydrolysing laminarin and alginates.

Habit group	Sources of cultures	Strains isolated		Hydrolysis of					
				Alginate only		Laminarin only		Alginate + Laminarin	
		B	A	B	A	B	A	B	A
1	Fresh *Fucus vesiculosus*	14	7			6	5	4	
2	Decomposed *Fucus vesiculosus*	1				1			
3	Decomposed *Laminaria digitata*	18		16		2			
4	Decomposed *Fucus serratus*	4				4			
5	Decomposed *Polysiphonia fastigiata*	4		4					
6	Decomposed *Gigartina mammilata*	3		3					
7	Sea-water	10	1			6	1		
8	Intertidal, black, organic mud	1						1	
9	Intertidal, black, sand	1	6				3	1	1
10	Lagoon mud	1	4				2		1
11	Salt marsh soil	2	3				2		1
12	Garden soil	3		2		1			
13	Air contaminant	2				2			
	Totals	64	21	25	—	22	13	6	3

B = Bacteria ; A = Actinomycetes.

Many of the active bacterial strains are closely related, but for the moment only approximate identifications have been made and these, along with certain biochemical characteristics of the strains are set out in Table II. It will be noticed that the most active strains [1, 13, 18] belong to the coryneform group of bacteria. Strains 1 and 18 also actively hydrolyse cellulose and calcium pectate and might therefore be expected to play some considerable part in the decomposition of seaweed thalli. Of these strains only 18 was recovered directly from a seaweed thallus [*Fucus vesiculosus*] ; 1 and 13 were isolated from intertidal sand in which mixed populations of seaweeds were decomposing.

These records consitute the first report of the hydrolysis of laminarin by bacteria.

At an early stage in this study, and during previous investigations of the activities of certain soil inhabiting micro-organisms, it was evident that many actinomycetes were able to attack insoluble laminarin and to utilize it as their sole source of carbon. From certain of the same habitats which provided the active cultures of bacteria, a series of active strains of *Streptomyces* were isolated. These are arranged in Table III under arbitrary groups depending on the colony colour on potato dextrose agar, on the pigment produced in the agar, and on the degree of diffusion of this pigment. As compared with bacteria, strains of *Streptomyces* decompose laminarin more actively and more consistently. There is little decrease in activity with prolonged cultivation on agar media.

Almost all the strains hydrolyse starch, gelatin and calcium malate, and some hydrolyse calcium pectate. Only one strain [IX] hydrolyses calcium alginate.

So far there are no published records available to the authors of hydrolysis laminarin by strains of *Streptomyces*, nor is any account known of the hydrolysis of an alginate by a member of this genus.

TABLE II.—Biochemical characteristics of certain laminarin decomposing bacteria.

Strains of Bacteria	Isolation number	Habit group	Hydrolysis of						
			Laminarin	Ca-alginate	Starch	Cellulose	Ca-pectate	Casein	Gelatin
Achromobacteriaceae	6	7	1	—	+	+	—	—	—
	14	2	1	—	—	—	—	—	—
	17	7	1	—	—		—	—	—
	20	1	1	-	—	—	—	—	—
	12	1	1	—	—	—	—	—	—
Flavobacterium type	22	1	1	—	—	-	—	—	—
Coryneform bacteria									
(a) *Persistent mycelium*	1	9	3	2	+	+	+	+	+
	13	9	3	3	—	—	—	—	+
(b) *Gram positive rods*	34	13	2	—					
(c) *Gram variable rods*	55	3	2	—					
	56	3	2	—					
	45	4	1	—					
(d) *Soil diptheroids*	10	1	1	—	—	—	—	—	—
	18	1	4	2	—	+	+	+	—
Bacillus [various]	3	1	2	—	—	—	—	+	+
	15	7	1	—	—	—	—	+	+
[Group II]	21	7	1	—	—	—	—	+	—
	4	11	2	—	+	+	—	—	+
[Group I]	54	3	1	—					
Bacillus polymyxa	33	13	4	—					

For laminarin and Ca-alginate, units represent the average width in millimetres of zones of hydrolysis after 14 days at 26°C :—1 = not over 2; 2 = 2–8; 3 = 8–12; 4 = 12–24; + = presence; — = absence of activity [blank spaces indicate absence of test].

Many of the strains of bacteria and of *Streptomyces* degrade sodium alginate solution [1·0 per cent] as measured by decrease in viscosity. At the present, attention has been confined to hydrolysis of calcium alginate, which is of more limited occurrence, because it can be demonstrated visually and the degree of activity of particular organisms can be assayed in agar culture.

LAMINARIN DECOMPOSITION.

The alginase isolated by Waksman & Allen (1934) from bacteria was demonstrated to reach its highest activity in solutions containing additional sodium chloride, and various workers have stressed the importance of increased salt content for media employed for the isolation of marine organisms. In so far as hydrolysis of laminarin suspended in Czapek-Dox, yeast extract agar is concerned, the addition of increasing amounts of sodium chloride to an effectively buffered medium, limits the activity of most of the strains investigated. Typical experimental results are given in Table IV.

The precise level of sodium chloride which significantly reduces the active decomposition of insoluble laminarin, as assayed by the width of the clear zone, varies with the organism but for four of the five strains hydrolysis still occurs in 2·0 per cent sodium chloride.

TABLE III.—Growth characteristics of certain laminarin decomposing strains of *Streptomyces*.

Strains of Streptomyces	Isolation number	Habitat group	Hydrolysis of						Growth on glycerine	Violet colour : litmus milk
			Laminarin	Ca-alginate	Starch	Ca-pectate	Ca-malate	Gelatin		
Growth on potato dextrose agar. Colony white : reverse brown, diffusing	I	1	3	—	+	—	+	+	+	—
	V	1	2	—	+	+	+	+	+	—
	VI	1	2	—	+	+	+	+	+	—
	VII	9	3	—	+	—	+	+	+	+
	XIV	9	3	—	+	—	+	+	+	+
	XV	9	2	—	+	—	+	+	+	+
	XVI	8	2	—	+	—	+	+	+	+
	XVII	8	4	—	+	—	+	+	+	+
Colony white : reverse brown, not diffusing	II	1	2	—	+	—	+	—	+	—
	III	8	4	—	+	—	+	+	+	+
	IX	11	3	2	+	+	—	+	+	+
Colony grey : reverse brown, not diffusing	X	1	2	—	—	—	+	+	+	—
	XII	11	2	—	+	+	—	+	+	+
	XVIII	13	3	—	+	—	+	—	+	+
Colony violet : reverse brown, diffusing	IV	7	2	—	+	+	+	+	+	—
Not growing on potato dextrose agar	XI	11	2	—	+	+	—	+	+	+
	XIII	9	1	—	—	+	—	+	+	—

For laminarin and Ca-alginate units represent average width of zones of hydrolysis in millimetres after 14 days at 26° C. :—1 = not over 5 ; 2 = 5–15 ; 3 = 15–25 ; 4 = 25–50. + = presence ; — = absence of activity.

Visible decomposition of calcium alginate by the bacterial strains 13 and 18 and by *Streptomyces* IX is limited by concentrations of sodium chloride in excess of 0·5 per cent and growth of these organisms fails at concentrations higher than 1·0 per cent.

TABLE IV.—Effect of concentration of sodium chloride on hydrolysis of insoluble laminarin expressed as width in millimetres of zones of hydrolysis after 7 days at 26° C.

Czapek-Dox, yeast extract agar + 2 per cent Laminarin		Plus NaCl per cent				
		0·0	0·5	1·0	1·5	2·0
Coryneform bacterium	1.	12·0	12·0	12·0	12·0	7·5
Bacillus	3.	5·5	5·5	2·0	2·0	0
Streptomyces	XII	3·5	3·5	6·0	6·0	3·5
Streptomyces	XIV	14·0	14·0	14·0	11·0	11·0
Streptomyces	XVIII	15·5	15·5	15·5	11·0	11·0

After autoclaving, insoluble laminarin does not precipitate in media of high pH value. Therefore, the visual assay of decomposition by bacteria and actinomycetes in media with pH values beyond 8·0 is not possible, but between approximately pH 8·0 and pH 5·5 there is a rapid falling-off in activity. This is demonstrated in Table V in which the initial and final pH values of Czapek-Dox laminarin agar with, and without additional sodium chloride are related to the width of the clear zone of hydrolysis stated in millimetres, after 8 days' incubation at 26° C.

TABLE V.—Effect of changes in hydrogen-ion concentration of media with and without sodium chloride on the hydrolysis of insoluble laminarin, expressed as width of zones of hydrolysis in millimetres after 8 days at 26° C.

	Czapek-Dox + 0·1 per cent yeast extract + 2·0 per cent laminarin No. NaCl				
Initial pH	7·80	7·36	6·85	6·80	6·08
Bacterium 13	(7·44) 24	(7·10) 23	(6·78) 17	(6·61) 8	(5·50) 0
Bacterium 18	(7·46) 22	(7·23) 21	(6·84) 12	(6·50) 0	(5·50) 0
Streptomyces IX	(7·40) 26	(7·32) 26	(6·96) 22	(6·74) 21	(5·90) 12
	Czapek-Dox-yeast-laminarin + 2·0 per cent NaCl				
Initial pH	7·46	7·13	6·75	6·54	5·57
Bacterium 13	(7·20) 22	(6·81) 19	(6·68) 18	(6·40) 6	(5·36) 0
Bacterium 18	(7·30) 20	(7·10) 21	(6·80) 12	(6·34) 4	(5·38) 0
Streptomyces IX	(7·21) 24	(6·96) 21	(6·58) 15	(6·36) 16	(5·47) 1

Final pH values given in brackets.

Most active hydrolysis occurs between approximately pH 7·0 and pH 8·0, and for the two bacterial strains, in both series of media, the more acid limits in which hydrolysis can occur are clearly defined. The actinomycete strain in the series lacking sodium chloride maintains a degree of decomposition even at the lowest values investigated.

The decomposition of insoluble laminarin in agar media proceeds at different rates according to the strain of organism producing the active enzyme and according to the pH value of the medium. A gradient of enzyme concentration exists through the agar from the growing edge of the colony and diffusion can be demonstrated in advance of visual clearing. A series of 4 mm. discs cut by a sterile cork-borer from a point immediately beyond the growing edge of the colony (1), from the middle of the clear zone (2), from the edge of the clear zone (3), from the turbid agar outside the clear zone (4), and from the unaltered agar (5), when placed on fresh laminarin agar produce zones of clear agar which give a measure of the concentration of the enzyme in the original disc. Results from one such experiment are set out in Table VI. Measurements of the zones of hydrolysis were made after 6 days' incubation at 26° C.

Table VI.—Demonstration of diffusion of laminarinase in advance of growing edge of colony.

		Distance from colony				
		1	2	3	4	5
Bacterium	1	16·5	15·0	9·5	6·0	5·0
	3	11·0	—	9·5	5·0	5·0
Streptomyces	XII	14·0	13·0	10·5	6·0	6·0
	XIV	21·0	16·0	7·5	6·0	6·0
	XVIII	16·0	12·5	6·5	0	0

Distance from colony in arbitrary units [see text]; width of zones of hydrolysis in millimetres.

With the exception of *Streptomyces* XVIII, the unaltered agar of zone 5 had already accumulated a certain concentration of the diffusing enzyme.

The activity of the enzyme increased with increase in temperature to at least 37° C. and diffusion from an agar disc from the middle of the initial clear zone (2) proceeds for at least six days after transfer to fresh agar. This is demonstrated in Table VII.

Table VII.—Diffusion of laminarinase in relation to tempertaure and time of incubation, expressed as width in millimetres of clear zones produced by discs cut from the middle of zones of hydrolysis round a bacterium and an actinomycete.

Bacterium 1			*Strephomyces* XIV	
15° C.	5·5	9·5	6·0	10·0
26° C.	9·0	16·5	9·5	16·5
37° C.	10·5	19·0	14·0	22·5
Hours	48	144	48	144

In view of the results set out in Table VI it must be realized that the measurements of the clear zones only indicate the width of visible hydrolysis and do not give an accurate estimate of the limits of diffusion of the enzyme.

Isolation of Laminarinase.

The first isolations of crude, cell free enzyme extracts capable of hydrolysing insoluble laminarin were made from the clear peripheral zones produced in laminarin agar by the growth of bacterium 18 and *Streptomyces* V. The clear agar from several plates was excised, due care being taken to prevent touching the growing colony, mixed with washed, sterile silver sand in the proportion of five parts of sand to one part of clear agar, and ground. The mixtures were freeze dried and stored at about −8° C.

Before each extraction the freeze dried material was tested for activity and found to be positive. Repeated extraction was carried out by a neutral phosphate solution (70 parts of 2/15 molar Na_2HPO_4 plus 20 parts of 2/15 molar KH_2PO_4) in the proportion of one part by weight of mixture to one part by volume of phosphate solution. The extracts were tested in penicillin assay cups on plates of insoluble laminarin agar incubated at 36° C. After 24 hours bacterium 18 gave zones of hydrolysis averaging between 13 and 14 mm. in diameter and *Streptomyces* V, zones of between 15 and 18 mm. in diameter. The extracts were cleared in a centrifuge for 15 minutes at 2800 revolutions per minute and retested, when some improvement in activity was obtained, bacterium 18 giving zones of hydrolysis averaging between 16 and 19 mm. in diameter; *Streptomyces* V zones between 21 and 23 mm. in diameter.

When the centrifuged extracts were mixed with absolute ethyl alcohol to give a final alcohol content of 75 per cent, a white precipitate was obtained. The mixtures were stored overnight at 5° C. and the precipitates were separated by centrifuging for 15 minutes of 3000 revolutions per minute. The precipitates were washed three times with 75 per cent ethyl alcohol and dried at 37° C. The dry precipitates were redissolved in distilled water and tested on insoluble laminarin agar. Zones of hydrolysis of 9 and 10 mm. diameter were obtained for *Streptomyces* V, and of 12 and 13 mm. diameter for bacterium 18. The supernatant alcoholic liquid was reduced in volume by vacuum distillation, but on testing against laminarin agar gave negative results.

A substantially similar series of extracts was prepared from the agar of the clear zones produced by bacterium 34 except that in this series extracts were obtained from the unaltered, peripheral agar. The final redissolved aqueous solution of the precipitate from the clear area gave zones of hydrolysis averaging between 25 and 30 mm. in diameter; the solution of the precipitate from the unaltered agar gave zones averaging 22 to 25 mm. in diameter, the temperature of incubation for both samples being 28° C. This extraction experiment confirms the results set out above in Table VI, that the enzyme produced by a colony diffuses well in advance of the visible zone of hydrolysis and demonstrates that the laminarinase can be recovered from apparently unaltered substrate.

A liquid medium containing 20 gm. insoluble laminarin, 1·0 gm. Difco yeast extract, 0·5 gm. KNO_3, 0·5 gm. $MgSO_4{\cdot}7H_2O$, 1·0 gm. K_2HPO_4, and a complete micro-element supplement and distilled water to give 1000 ml., was dispensed as 25 ml. quantities in 100 ml. pyrex flasks. Inoculated with *Streptomyces* IX, thirty of these flasks were incubated at 28° C., being shaken twice each day during the five weeks necessary to hydrolyse the insoluble laminarin. The actinomycete mycelium was filtered off on a ×5 grade sterile sinter glass filter. When the filtrate was treated with absolute ethyl alcohol to give a 75 per cent by volume concentration of alcohol, a white precipitate was thrown down. The precipitate was removed by centrifuging, washed with 75 per cent alcohol, collected on sterile filter paper and dried at 37° C. Portions of the precipitate were extracted with sterile distilled water and the extracts tested on insoluble laminarin agar at 28° C. for 24 hours when zones of hydrolysis averaging between 16 and 19 mm. in diameter were obtained. Again the supernatant alcoholic liquid gave negative results when the residue was tested after vacuum distillation.

A similar, but more extensive experiment, in which 1000 ml. volumes of the culture liquid were precipitated with alcohol was carried out. In this, the precipitate from one 1000 ml. of culture liquid was treated as described above, while the precipitate from a similar volume was dissolved in water immediately after filtration and was then reprecipitated with alcohol, collected and treated as described above. On test at 28° C. for 24 hours on insoluble laminarin, the extract from the former gave zones of hydrolysis averaging between 11 and 12 mm. in diameter, that from the latter, zones of 11 to 17 mm. in diameter, there being little significant improvement in activity due to the reprecipitation of the enzyme containing material.

ISOLATION OF AN ALGINASE.

Using a medium consisting of the mineral salts of Czapek solution with 0·2 per cent yeast extract and a mixture of 1·0 per cent sodium and 1·0 per cent calcium alginate as the carbohydrate source, and a complete micro-element supplement, 20 ml. volumes of solution were distributed in 100 ml.

conical flasks. These were inoculated in sets with bacterial strains 1 and 13 and with *Streptomyces* IX and XIX, and incubatedat 24° C. for nine days. The initial solutions were viscous and contained a finely divided suspension of calcium alginate. At the end of the incubation period the flasks containing bacterium 1 and *Streptomyces* XIX showed little if an change in viscosity and extraction tests failed to reveal measurable quantities of alginase. The viscosity of the culture liquid, on which bacterium 13 had been growing, had been greatly reduced, but the calcium alginate was still present as a sediment. There was a similar reduction in viscosity in the culture liquid inoculated with *Streptomyces* IX, but the calcium alginate had completely disappeared. Subsequent extractions and assays of the cultures of bacterium 13 provided evidence of only slight alginase activity, but such activity was easily demonstrable for cultures of *Streptomyces* IX. Extraction of the latter cultures was carried out in the following steps. The cultures were filtered through filter paper and the mycelium was retained. The filtrate was treated with 35·0 per cent $(NH_4)_2SO_4$ and a precipitate recovered by filtration. Dissolved in glass distilled water this precipitate gave active hydrolysis of insoluble laminarin but showed no activity against calcium alginate suspended in agar.

Thereafter, the *Streptomyces* mycelium was repeatedly extracted with the same volume of 15·0 per cent ethyl alcohol and the extract treated with sufficient absolute alcohol to yield a total concentration of 60 per cent. The precipitate which formed was collected by filtration, washed with 60 per cent alcohol and dried overnight at 37° C. The precipitate was treated with glass distilled water, the extract obtained being filtered through a glass Seitz filter. This extract on assay on calcium alginate agar plates at 28° C. for 48 hours gave zones of hydrolysis varying from 20 to 22 mm. in diameter, but was inactive on plates of insoluble laminarin. Added to sodium alginate solution in proportions of one part of extract to seven parts of a 1 per cent alginate solution, viscosity was considerably reduced after 24 hours' incubation at 28° C. and a gel was not formed by treating the incubated solution with 4 per cent calcium chloride. Thus, the mycelium of *Streptomyces* IX, developed on a medium containing alginates as a sole carbohydrate source, on extraction with alcohol yields a precipitate which contains a water soluble fraction which hydrolyses both sodium and calcium alginate. Stored at 1° C. after Seitz filtration this extract retained its activity for at least two weeks.

The experiments with *Streptomyces* IX were repeated using media of the same composition in larger volumes and incubating for 14 days at 24° C. The filtrate from the bulked culture liquids and the total mycelium produced were extracted, precipitated, and tested. In every instance the precipitate initially developed was dissolved in glass distilled water, and reprecipitated with 75 per cent alcohol, so as to purify in some degree the final precipitate which was tested in aqueous solution. The purified precipitate obtained from the culture filtrate was only slightly active against calcium alginate, but extracts of the mycelium were again quite active. The mycelium was first extracted with 35 per cent $(NH_4)_2SO_4$ and the extract dialysed through a cellulose membrane for 48 hours before precipitation in 75 per cent alcohol. This same mycelium was then extracted with 15 per cent alcohol at 37° C. for 24 hours and the precipitate, formed by addition of alcohol to yield a final concentration of 75 per cent, was dissolved in distilled water and purified by reprecipitation in 75 per cent alcohol. On assay against calcium alginate agar these mycelial extracts gave zones of hydrolysis averaging between 19 and 20 mm. for the ammonium sulphate extract, and between 13 and 14 mm. for the alcoholic extract. No laminarin activity was demonstrated.

Our experience with both bacterial and actinomycete strains, which at isolation give indication of alginase activity, is that the latter, because of the larger bulk of living material which is obtainable in culture, are better subjects for the extraction of an alginase.

Fungi Capable of Hydrolysing Insoluble Laminarin.

Up to this stage of the investigation detailed examination of the laminarinase activity of fungi associated with decaying seaweeds has not been possible, but it may be of interest to record that very few species of the many which grow on decomposing seaweeds possess such activity. *Trichoderma viride* Pers., *Penicillium spinulosum* Thom, *Geomyces*, possibly *G. cretaceus* Traaen, and a species of *Cephalosporium* are all capable of hydrolysing insoluble laminarin as demonstrated by clear zones round the margin of the colonies growing on agar, but the rate of hydrolysis is slow as compared with the most active bacterial and actinomycete strains. It is higher, however, than the activity of the weaker strains of the latter organisms. Alginase formation as measured by hydrolysis of calcium alginate does not occur, but there is evidence of a degree of hydrolysis of sodium alginate as measured by loss of viscosity of a 1 per cent solution and by failure in gel formation when culture filtrates are treated with 4 per cent calcium chloride.

Conclusion.

As might be expected from its chemical structure, the decomposition of insoluble laminarin by micro-organisms is a more widespread phenomenon than the decomposition of sodium and of calcium alginates. McNaught, Smith & Black (1954) have demonstrated that laminarin, and the frond of *Laminaria cloustoni*, stimulated to vigorous activity the mixed microflora of the bovine rumen. The isolated laminarin, and presumably the laminarin of the seaweed frond, were readily utilized by the constituent elements of this flora. Within the limits of their experiments no attempt was made to assess the part played by particular organisms of the flora, but it is highly probable that bacteria played a considerable part in the conversion of the laminarin The present work indicates that not only bacteria, but also actinomycetes and fungi can hydrolyse insoluble laminarin, and that cell-free filtrates from culture liquids of appropriate bacteria and actinomycetes actively decompose insoluble laminarin. A reasonably pure and stable solid containing the laminarinase can be precipitated by alcohol from such filtrates. At the moment, it would appear that actinomycetes yield more active extracts than do bacteria. The enzyme is most effective in neutral or slightly alkaline solutions at temperatures between 37° and 40° C.

Decomposition of sodium and calcium alginates is a less common phenomenon of micro-organisms from the habitats studied, and has not yet been fully confirmed for fungi. This agrees with the work of Waksman and his associates. So far we have had only partial success in isolating an alginase from the culture liquids of bacteria and actinomycetes which have a clearly positive reaction against calcium alginate suspended in agar. An active alginase-containing powder has been obtained by extracting the mycelium of an actinomycete with alcohol and with ammonium sulphate, and this alginase has been demonstrated to hydrolyse calcium alginate. Our work indicates that hydrolysis of sodium alginate may be more widespread than hydrolysis of calcium alginate, but final results are not yet available.

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TAXONOMIC STUDIES ON THE TUBER-BEARING SOLANUMS. 1: SOLANUM TUBEROSUM AND THE TETRAPLOID SPECIES COMPLEX

By J. G. Hawkes.

(With Plates 2 to 5 and 8 text-figs.)

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1. Introduction.

Much has been written on the affinities of the European potato, and several legends have arisen about its place of origin and the time of its introduction. At the present day, however, thanks to the works of Sabine (1824), Mitchell (1886), Roze (1898), Wittmack (1909), Wight (1916), Salaman (1937) and others we are left in little doubt about the main botanical and historical facts.

We know that the potato came from South America in the latter part of the 16th century and that two distinct introductions were made, one into Spain and the other into England. Yet the exact point of origin of these first European potatoes is still a matter for controversy, and the 'original wild potato' has not yet been found; indeed it may not now exist.

The detailed taxonomic works of Bitter (1911–1913), of Juzepczuk and Bukasov (1929), and of Bukasov (1930, 1933) have done much to elucidate problems of distribution and variation within the cultivated potatoes of South America and have certainly stimulated great interest in the problem. The taxonomic methods and conclusions of the Russian botanists, however, are open to serious criticism, especially as none of their type material has been made available to western botanists for further study. Both Bitter and the Russian school considered it necessary to split their material up into several hundreds of small species, often grouped under various " collective species ". Genetical and plant-breeding studies indicate, however, that there is no justification whatsoever for this procedure, and that most of the microspecies are no more than clones ; this is also brought out by more detailed studies made on herbarium material alone, when, in recent times, more material has become available for study.

I am quite convinced that the only way of creating some sort of order out of the chaos into which potato taxonomy has been thrown is to consider the species as very large ones, with a wide range of infra-specific variability. At any level below that of the subspecies this variability is not analysable by classical botanical techniques, or only to a very limited extent. This is due, I think, to the fact that both wild and cultivated potatoes in South America reproduce sexually and are most of them obligatorily cross-pollinated, so that the variability within the species is being continually mixed up and presented in fresh combinations ; only in the case of the geographical and altitudinal subspecies does it become more sorted out, fixed, and characteristic.

Another factor that must be taken into account in a study of the taxonomy of potatoes is the alternative method of reproduction, which is strictly analogous with the phenomenon of facultative apomixis in *Rubus*, *Hieracium*, and other genera. An individual that is formed as a sterile hybrid between two species, or as an autopolyploid or an unbalanced allopolyploid, or, from whatever other cause, has a very reduced fertility, is able to survive indefinitely by vegetative clonal reproduction, whilst in an exclusively sexually reproducing genus it would not survive beyond the first generation. Many of these sterile clones have been given specific rank in the past, a practice which I consider to be just as reprehensible with *Solanum* as it is in the case of the apomictic genera, since it clutters up the literature with thousands of names of forms that have no relation whatsoever to the generally accepted modern concept of the species.

The work of Bitter, and to some extent that of Juzepczuk, suffered greatly in that it was confined to a study of dried herbarium material. It is now well known that the environmental plasticity of most potato species is very great, so that studies based on herbarium material alone are apt to place too much emphasis on differences due to changes of environment. In any case the time is or should be well past when any of our major crop plants could be classified by studying dried herbarium material, without reference to cytological and genetical studies. The experimental method, as we shall see below, is of the greatest value, in helping to define specific boundaries and in studying the range of infra-specific variation.

It is my purpose in the present series of taxonomic papers to link up in this way the results of my own and of other workers' experimental studies with past treatments of the taxonomy of this group of plants and with the data obtainable from the thousands of sheets of herbarium material from all parts of the world that I have been able to examine.

In this first paper I shall deal with the most important of all the tuberous Solanums, namely, the tetraploid cultivated potato of Europe, *S. tuberosum* L. and its near relatives.

I wish to take the opportunity of recording here my grateful thanks to Dr. T. A. Sprague for help and advice on the selection of a suitable type for *S. tuberosum ;* to Mr. S. Savage for data on the specimens in the Linnaean Herbarium ; to Mr. T. O'Grady for kindly obtaining a photograph of the type specimen and for help with a number of literature references ; to the

Commonwealth Bureau of Plant Breeding and Genetics, Cambridge, for translation of Russian works ; and also to Miss E. Koutaissoff, Lecturer in Russian Language at Birmingham University, for so kindly elucidating the intricacies of style and meaning in many of the passages in the works of the Russian taxonomists with which I have had to deal. My grateful thanks are due also to Dr. G. Taylor and Mr. J. E. Dandy for reading through the present manuscript and giving me the benefit of their advice and criticism.

2. Place of Origin of the European Potato.

There are no historical records which give the exact year of introduction of the potato into Europe. Salaman (1937), however, considers that it probably arrived in Spain a little earlier than 1570 and in England a decade later, though from a separate source.

There is no complete agreement either as to the part of South America from where the potato was taken into Europe. Juzepczuk and Bukasov (1929) and Bukasov (1933) consider, on the basis of morphological and physiological studies that it must have been derived from southern Chile. Nevertheless, this is denied by Salaman (1937, 1946) and Hawkes (1944) on historical and on botanical grounds. These authors think it much more likely that the potato was brought from the Andes mountains, either from Peru–Bolivia, or from Colombia. We shall consider the evidence for these hypotheses in more detail later. There is no doubt, however, that the potato was grown in both Spain and Italy in the last decades of the 16th century, and was received by the botanists of the day as an interesting curiosity.

3. Early Botanical Studies.

Although the potato was described by the early Spanish chroniclers such as Pedro Cieza de Léon (1553), Acosta (1590), Garcilasso de la Vega (1609) and many others, these accounts were not by any means botanical descriptions and are of no value to us in trying to obtain an idea of the botanical variation of the potato in its ancient home.

We have, however, several very detailed descriptions of the early European potatoes made by the botanists and herbalists Caspar Bauhin (1596, 1598 (in Matthiolus), 1620, 1623), Clusius (1601), Gerard (1597), Jean Bauhin (1651), Dodoens (1644), and Parkinson (1629, 1640).

Of these, undoubtedly the most accurate and useful descriptions were those of Caspar Bauhin and Clusius. To Caspar Bauhin, incidentally, goes the honour of having published the first botanical description of the potato, though as he probably received his specimens from Clusius, we cannot be sure when the descriptions were actually made. Bauhin also made a herbarium specimen of the potato which is still preserved in excellent condition at the Basle Herbarium in Switzerland (see Pl. 3). In his *Phytopinax* of 1596 he not only places the potato in the genus by which we know it today ; he also names it in exactly the same manner, that is to say he gives it the binomial *Solanum tuberosum*. However, in his later works of 1598, 1620 and 1623 he adds the word *esculentum* (see fig. 1) and it was this trinomial that seems to have been taken up by later authors.

Bauhin's contemporaries were not inclined to follow his nomenclature for this plant and most prefer to use latinized forms of vernacular names such as ' Battata Virginiana sive Virginianorum ' (Gerard, 1597), ' Papas peruanorum ' (Clusius, 1601), ' Arachidna Theophrasti ' (Clusius, 1601), etc., etc. The word Battata from which our name *potato* was derived was originally taken from the vernacular name of the Sweet Potato (*Ipomoea batatas*), whilst the word ‘ Papas ’ is the hispanicized plural of the South American Quechua word for the potato, obtained from Cieza de León. Clusius considers that our plant might have been Theophrastus’ ‘ Arachidna ’, a plant whose identity is not certain and which, in any case, can have no relationship to the potato.

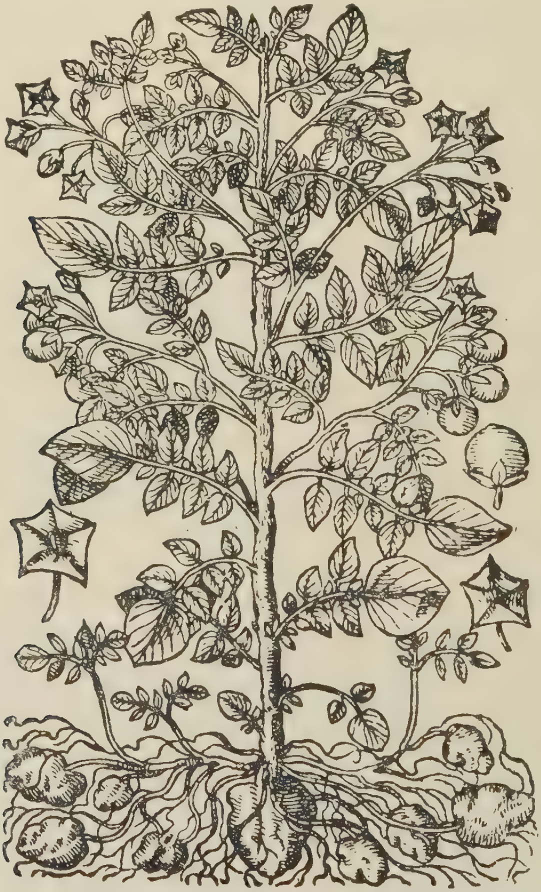

Fig. 1.—‘ Solanum tuberosum esculentum ’. The cultivated potato, figured by Caspar Bauhin in his *Prodromus* of 1620. Although the representation is somewhat stylized it is of interest to note the abundant flowers and berries, the long stolons and irregular tubers, all characteristic of subsp. *andigena*. The presence of sobols is common in this short day adapted species when grown in the long summer days of Europe.

Later botanists, such as Ray (1686), Tournefort (1719) and Boerhaave (1720), all refer to Bauhin’s *Prodromus* of 1620, in which the trinomial *Solanum tuberosum esculentum* is given.

4. Linnaeus’ Descriptions.

Linnaeus’ first descriptions of the cultivated potato were published in *Hortus Cliffortianus* and later in *Viridarium Cliffortianum*, both of which appeared in 1737. The *Hort. Cliff.* description may have been made from living or dried specimens, but that of the *Vir. Cliff.* must necessarily have been made from living material, since in the latter publication only living plants grown at

Hartecamp, Holland, between the years 1735 and 1737 were described. Since no specimen of *Solanum tuberosum* appears in the Clifford Herbarium, housed now at the British Museum, it seems fairly safe to assume that Linnaeus' first description was made on the basis of living plants grown in Clifford's garden, and on the descriptions and figures of earlier botanists to which we have already referred.

Linnaeus' descriptions were extremely short compared with those of Bauhin and others, but references are given to the earlier works, so that the student could presumably refer to these if more information was required.

The description and references from *Hort. Cliff.* are given below :—
p. 60

[tuberosum]* 2. *Solanum* caule inermi [herbaceo] annuo, foliis pinnatis, pinnis integris.
Solanum tuberosum esculentum. *Bauh. pin.* 167.
prod. 89. t. 89 Moris hist. 3. p. 522. f. 13. t. 1. f. 19
Tournef. inst. 149. *Boerh. Lugdb.* 2. p. 67.
Arachidna theophrasti ? Papas americanorum.
Clus. hist. 2. p. 79.
Papas americanum. *Bauh. hist.* 3. p. 621.
Solanum tuberosum esculentum, flore albo.
Tournef. inst. 149.
Crescit in America.

The *Vir. Cliff.* version of the description differs only very slightly. The plant is spoken of as ' herbaceous ' and not ' annual ', and the leaves as having ' completely entire ' leaflets, as follows : (p. 15) *Solanum* caule inermi herbaceo. foliis pinnatis integerrimis. 60.2†.

It is of interest to note that the specific epithet '*tuberosum*' is not given in these two descriptions, though Linnaeus later added this in his own copy of the work. In the references, Linnaeus cites Bauhin's *Pinax* (1623) and *Prodromus* (1620) but strangely enough makes no reference to the *Phytopinax* of 1596. Morison's " Plantarum Historia Universalis Oxoniensis " (1680–99) is also referred to, the description and plate in this work being largely based on those of C. Bauhin. Linnaeus also quotes Tournefort (1719) in which no actual description is given, though a white-flowered form is also mentioned. The work of Boerhaave (1720) is quoted, though again no description was given. Clusius' work and the names mentioned by him are cited, and it is worth remembering that the descriptions of both Bauhin and Clusius are very detailed and of considerable value even by modern standards.

The next publication of Linnaeus which mentions the potato is the *Hortus Upsalensis* (1748), in which is given a list of the plants grown by Linnaeus in the Uppsala Botanic Garden between the years 1742 and 1748. The description is the same as in *Vir. Cliff.*, and the usual references are added to Bauhin's trinomial *Solanum tuberosum esculentum* and to the names given by Clusius. In addition he notes the vernacular Swedish names and country of origin, as follows :

p. 48 *Svecis* Jord-paeron, Potatos
Habitat, ut fertur, in Virginia
Hospitatur *sub dio,* & vulgaris in *Hortis,* annuum, ex tuberibus propagandum.

From this we gather that the potato was a commonly grown plant in Sweden during the period 1742 to 1748, and was propagated from tubers in the usual way.

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* Words in square brackets were inserted in Linnaeus' handwriting in his own copy in the Library of this Society.

† Refers to page and number in *Hort. Cliff.*

The reference to its native country must have been taken either directly or indirectly from Gerard, though no reference is cited. We know now, of course, that the potato did not originate in Virginia, neither was there any wild native potato to be found within thousands of miles of that region.

We now come to the description in the ' Species Plantarum ' of 1753 in which the binomial *Solanum tuberosum* is first used by Linnaeus. Apart from the name there is nothing in this description that has not already appeared in the other publications of Linnaeus, and we quote it here only because of its value in being the starting point for botanical nomenclature and hence the first valid and legitimate publication of the name *Solanum tuberosum* according to the International Code.

p. 185

8. *Solanum* caule inermi herbaceo, foliis pinnatis integerrimis. *Vir. Cliff.* 15. *Hort. Cliff.* 60. *Hort. ups* 48. *Roy. lugdb.* 423. *Dalib paris* 73. *tuberosum*
Solanum tuberosum esculentum. *Bauh. pin.* 167. *prodr.* 89. t 89.
Habitat in Peru. ⊙—♃

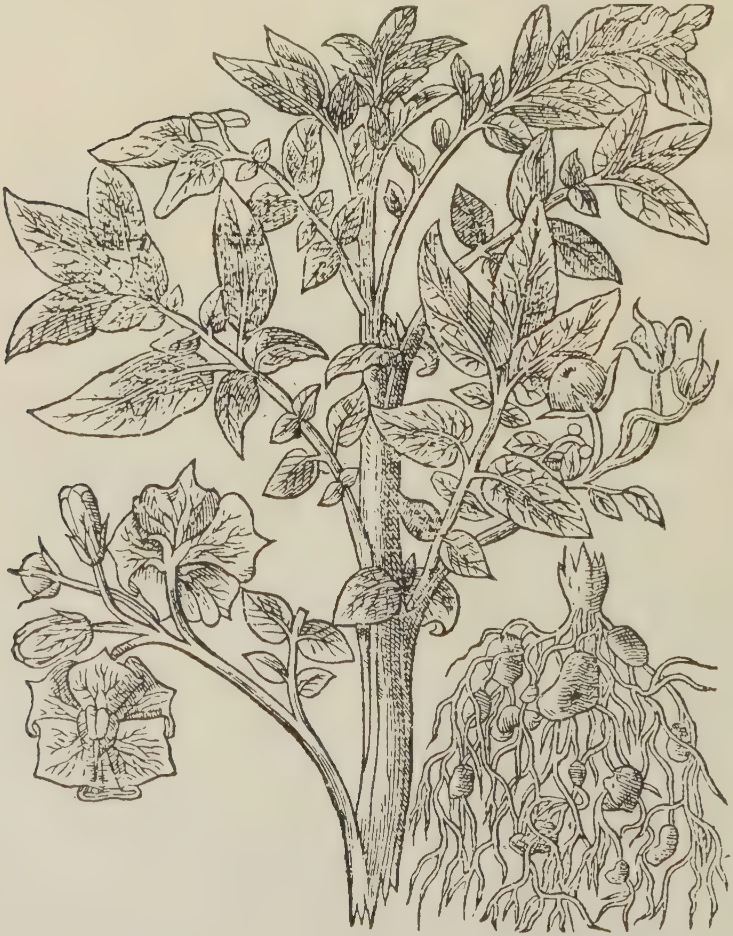

FIG. 2.—' Battata Virginiana '. Gerard's plate of *S. tuberosum* (*The Herball*, 1597). Note the small tubers, characteristic of subsp. *andigena* when grown in Europe.

In the second edition (1762) p. 265, the words ' penduncculis subdivisis ' and ' *innotuit* 1590 C. Bauhino ' are added. The descriptions of Adrian van Royen (1740) and Dalibard (1749) referred to in the above description are identical with and presumably taken from the descriptions in Linnaeus' earlier works. They are therefore of no further interest to us here.

Summing up the various descriptions of Linnaeus we can see that they were so constructed as to enable the botanist to distinguish the species of *Solanum* known in Europe at that time, and obviously are of no value, as we shall see later, in distinguishing the many species brought to Europe subsequently.

Linnaeus' concept of the species described in ' Species Plantarum ' was not a narrow one, based on a type specimen, but was formed as a result of studying a wide range of material ; and his descriptive phrase or polynomial was intended to embrace the variability of that species. There is little doubt, therefore, that in this case his description was based, not only on living plants seen by him personally in Clifford's Garden at Hartecamp, Holland, and in the Uppsala Botanic Gardens, but also on the descriptions and figures of Bauhin and Clusius, and possibly also of Gerard (see figs. 1 and 2).

It is known that during his visit to London in 1737 Linnaeus examined the Sloane and the Plukenet collections. He also visited the Sherard Herbarium in Oxford in the same year. In all these, 17th century specimens of the cultivated potato are now to be seen, as also in the Vaillant collection at Paris, which Linnaeus visited in 1738. It is very possible therefore that Linnaeus saw the potato specimens in these herbaria and that they also helped to form his concept of the species.

We can be confident in our assumption therefore, that Linnaeus took Caspar Bauhin's name *Solanum tuberosum*, using it to cover :

(1) The plants described and figured by previous authors, whom he cited.

(2) Potato plants cultivated in Europe up to 1753, actually seen by him either in a living or dried state.

Since in Linnaeus' day the type concept had not yet been formulated we are here faced with the problem of deciding on the type for the species *Solanum tuberosum*, bearing in mind that there is a wide range of variability between the accounts and specimens of Bauhin on the one hand and herbarium material taken in the 1750s on the other.

5. THE TYPE SPECIMEN OF *SOLANUM TUBEROSUM*.

It would have been of great value and interest if a specimen of the potato had been found in the Clifford Herbarium, but unfortunately none seems to have been preserved.

We have available to us, however, the classic herbarium made by Linnaeus himself, housed in the rooms of this Society, and these include specimens of *S. tuberosum* which I have examined in some detail.

There are three specimens so named in the herbarium, and I am indebted to Mr. Spencer Savage, former Librarian and Assistant Secretary of the Linnean Society, for historical and explanatory data in connection with these. The sheets are as follows :

(1) 248·12* (see Pl. 2 and fig. 3). Linnaeus has labelled it as ' 8 tuberosum ' (i.e. the number in Sp. Pl. ed. 1). Furthermore, according to B. D. Jackson's Index (1912) a specimen of this species was indicated by Linnaeus in his so-called ' first enumeration ', dated by Jackson as 1753. There is no evidence, however, that Linnaeus had this specimen, when he wrote Hortus Cliffortianus. It is a typical European potato variety, and, as we shall see later, is quite unlike Bauhin's or Boerhaave's specimens.

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* Code number given to sheet by Linnean Society for photographic record purposes.

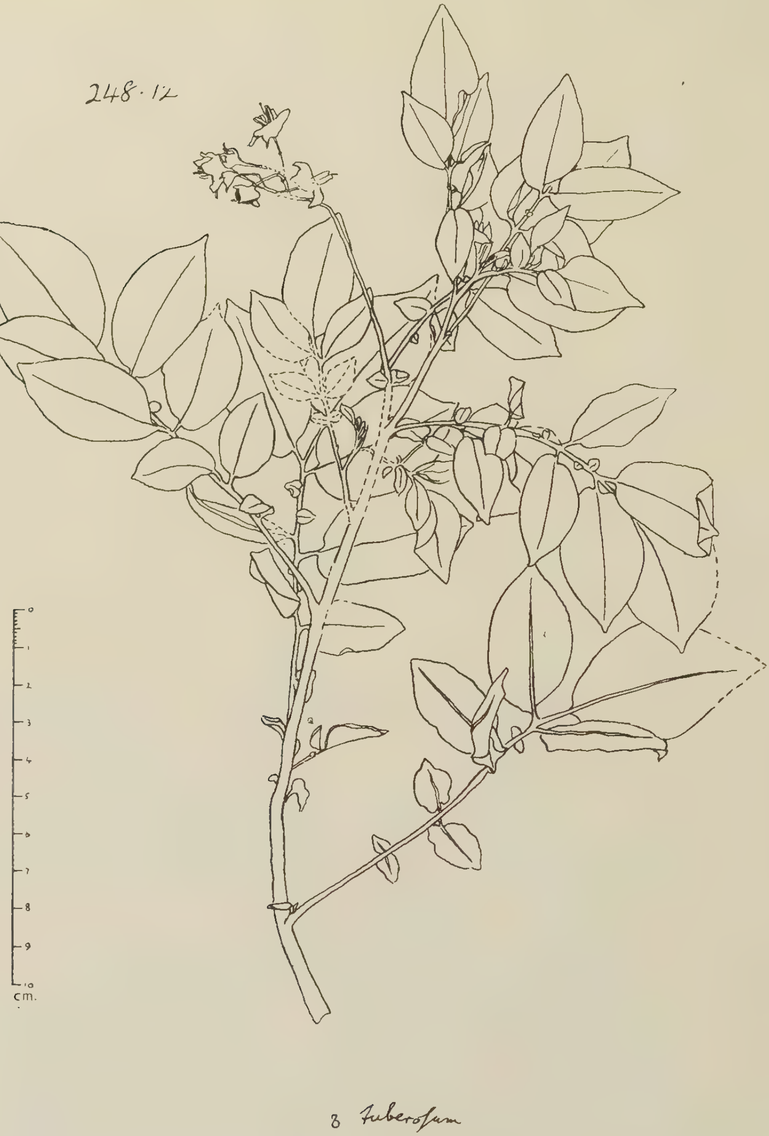

Fig. 3.—*Solanum tuberosum* L. Lectotype in Herb. Linn., No. 248·12. The damaged portions are indicated by dotted lines.

(2) 248·13. This sheet has been labelled by Linnaeus as ' tuberosum Mutis ' but does not in fact come within the present-day concept of *Solanum tuberosum*. The sheet also bears a number ' 125 ' which is in the handwriting of the celebrated botanist, astronomer and mathematician, José Celestino Mutis, who made extremely detailed collections from the then Spanish colony of New Granada, now the Republic of Colombia, South America. The number ' 125 ' can be traced to a manuscript list of Mutis of about 1773 and although no identification or collection data were given we know that Mutis was in and around the city of Santa Fé de Bogotá from 1770 to 1777. Between 1766 and 1770 Mutis was further north, in the region of Pamplona, but it is thought that he made no

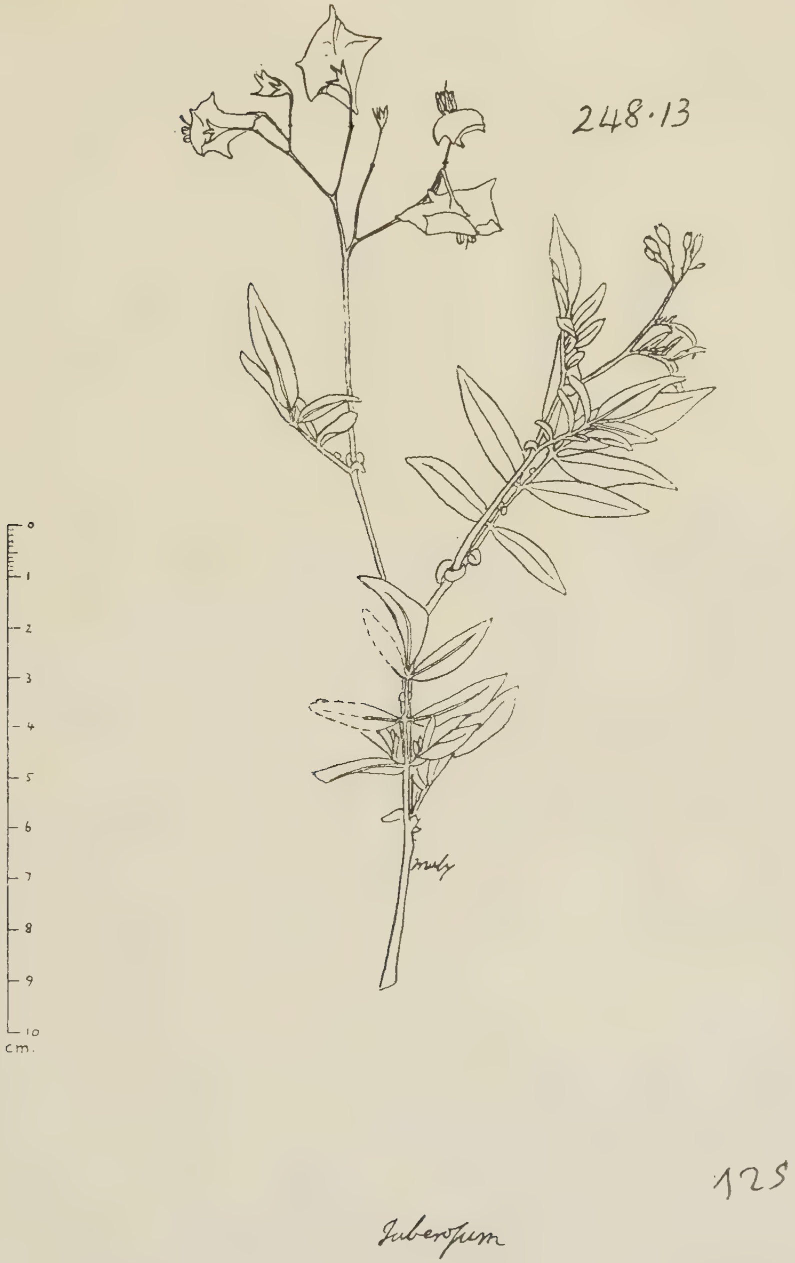

Fig. 4.—*Solanum colombianum* Dun. in Herb. Linn., No. 248·**13**. Collected by J. C. Mutis in the region of Santa Fé de Bogotá (No. **125**).

collections from this latter region. It is thus reasonable to suppose that the specimen in question came from Bogotá. It is a wild potato and undoubtedly comes within the species *Solanum colombianum* Dunal (see fig. 4), rather than *Solanum tuberosum* as we know it today. Furthermore, it was collected some

20 years *after* the publication of ' Species Plantarum ', and can therefore be dismissed as having had any influence on Linnaeus in his concept of *Solanum tuberosum* in the year 1753. That he later classified Mutis's plant with *S. tuberosum* is merely a reflection on the short description in ' Species Plantarum ', which would apply also equally well to 80 per cent of the wild potato species known at the present day.

(3) 248·14. The third specimen is labelled by the younger Linnaeus ' Solanum tuberosum? ' and bears also the words ' Coll. 2 da ' (=second collection received from Mutis). Mutis himself numbered the sheet ' 63 *Solanum* ', which is number 63 in the list in Mutis's handwriting, dated 1777. This specimen also very probably comes from Santa Fé de Bogotá, but it is very doubtful whether Linnaeus himself saw the plant, since he died in 1778, only one year after Mutis's list was prepared. It is recorded that he was too ill to examine this second collection of Mutis, entrusting its arrangement to his son. In any case the specimen in question is not *S. tuberosum* but must be placed with *S. caripense* Kunth, a non-tuberous relative which occurs abundantly in the environs of Bogotá, a fact to which the present writer can amply testify.

We are therefore concerned, in our discussion of the type of *S. tuberosum*, with only one specimen, namely the one labelled 248·12, since the second one was received from Mutis after the publication of ' Species Plantarum ' in 1753 and the third was probably not seen by Linnaeus at all. In any event, the last two plants represent wild species that could not possibly be included under *S. tuberosum* now that the full range of variability in the genus *Solanum* is more fully understood.

It thus seems evident that specimen number 248·12 had been seen by Linnaeus before the publication of ' Species Plantarum ' and we can safely assume that he had this (as well as other specimens, descriptions and plates) in mind as a basis for his description in that publication. The specimen furthermore agrees in all respects with this description, and I therefore consider that it should be selected as lectotype for the species :—

S. tuberosum L. Lectotype : Specimen number 248·12
labelled " 8 *S. tuberosum* ". In Herb. Linnaeus at
the Linnean Society's rooms, London, England.

Since the description in ' Species Plantarum ' is, as we have said before, extremely short, I am adding below a more detailed description taken from the type specimen in order to conform with modern taxonomic standards.

S. tuberosum L.

(Description made from the type specimen : 248·12 in Herb. Linn.) *Stem* : up to 22 cm. long, but probably much longer, to 4 mm. diam., slightly winged. *Leaves* : somewhat arched, standing at an angle of about 60° from the stem, 4-jugate, with 1–2 pairs of interjected leaflets ; leaf dimensions up to 14 × 7 cm.; lateral leaflets gradually diminishing in size from apex to base of leaf, ovate, somewhat acuminate, slightly oblique at the base, up to 42 × 22 mm., with short petiolules about 2–4 mm. long ; terminal leaflet larger than laterals, broadly ovate, acuminate, to 52 × 31 mm.; interjected leaflets minute, broadly ovate, sessile, up to 3 mm. long ; all parts of leaves and stems provided with rather frequent short hairs ; small pseudostipular leaves developed in leaf axils, attaining a length of 8 mm. or less. *Inflorescence* : few (–6)-flowered, at first terminal, later pushed to one side by a branch growing from the axil of the penultimate leaf ; peduncle furcate, 6 cm. long below and about 5–8 mm. long above the fork ; pedicels short, 8–11 mm. long, articulated at or slightly below the centre ; both peduncle and pedicels are provided with very sparse short hairs. *Calyx* : small, about 5 mm. diam., with short broadly ovate lobes and fairly well delimited acumens, the latter 1–2·5 mm. long. *Corolla :* apparently small, to 1·5 cm. diam. (but not well preserved and may therefore have been larger), possibly originally pinkish mauve in colour. *Androecium :* anthers 4–5 mm. long. *Gynoecium :* style possibly about 6–7 mm. long ; stigma capitate, not much larger than style apex. *Berry :* only small immature berry seen, 5 mm. diam ; two other flowers apparently fertile and beginning to set berries judging by the appearance of calyx and pedicel.

Unfortunately, the specimen has been somewhat eaten by insects, probably during the period between Linnaeus' death in 1778 and the time when the collections were sold to James Edward Smith in 1784. The pedicels and part of the stem are in especially poor state of preservation, yet despite this fact it seems obvious that Linnaeus' own specimen should be designated as the lectotype for the species. In the tracing (see fig. 3) that I have made of this specimen I have attempted, in so far as was possible, to reconstruct the damaged parts, indicating this by means of dotted lines.

6. The Modern Concept of *Solanum tuberosum*.

We have already mentioned that Linnaeus' descriptions of *S. tuberosum* emphasized only those special features which differentiate this species from the non tuber-bearing members of the genus. During the last 150 years very numerous collections of wild and native cultivated potatoes have been obtained in South America, and these have been classified into as many as 200 distinct species. To fully 80 per cent of these Linnaeus' descriptions would apply, though we can be quite certain that, had these potatoes been available to him, he would have regarded a large part of them as distinct from the cultivated potato.

The description we have given above, taken from the type specimen, will indeed separate *S. tuberosum* fairly well from the wild species. Nevertheless, this cannot obviously be considered as covering the full range of *S. tuberosum* itself, and it therefore becomes necessary to try to construct one which comprehends the full range of variability of this most variable species, at the same time separating it from the most nearly related wild and cultivated ones.

This task, having in mind the variation to be seen in South American potatoes and those now grown in all parts of the world, and the extreme environmental plasticity of the species, is not by any means an easy one. In addition, there is little doubt that some gene flow takes place in South America between *S. tuberosum* and several nearly related wild and cultivated sorts growing in the same areas. The following description is, therefore, a preliminary one, and will probably need to be modified in certain particulars at a later date.

S. tuberosum L. Sp. Pl. 1, p. 185.

S. parmentieri Molina, ex Walp. Rep. iii. 38 (*nom. nud.*)
S. esculentum Neck. Delic. Gallo–Belg. i. 119 (1768)
S. aracatscha Bess. Cat. Pl. Hort. Crem. (1816) 135 ; et ex Roem. & Schult. Syst. iv. 669 (1819) (*nom. nud.*)
S. sinense Blanco, Fl. Filip. ed. I. 137 (1837)

Plant : herbaceous, tuberiferous, with stolons which vary in length from very short (±1 cm.) to perhaps two metres according to variety and day-length ; average length about 5–10 cm. ; white or pigmented with anthocyanin.

Tubers : varying enormously in size, shape, colour, flavour and nutritive value ; size ranging from about 2 cm. to perhaps up to 20 cm., the usual range between 6–12cm. ; shape varying from orbicular through irregular isodiametric, ovoid, fusiform, cylindrical, to long and twisted or even vermiform, bent round on themselves ; surface smooth or irregularly indented or deeply indented at eyes and often swollen between ; skin colour varying from shades of dirty white (but this rarely and only in weed forms) through pale browns and yellows, pink, red, mauve, purple, deep purple, or black, often in the latter case with a leaden tinge ; pigmentation sometimes evenly distributed ("self"), or stippled, mottled or splashed, or to be found excluded from elliptical or semi-lunar regions round eyes (' spectacled '), or confined to regions round eyes or just at the base of the eye depression ; very rarely red and purple pigment types found in same tuber ; pigment found *either* in the cork *or* in outermost cortical layers, rarely in both ; flesh varying from grey-white (chiefly in weed forms) to white and shades of cream, lemon-yellow and deep saffron-yellow ; any of these shades may be tinted in addition with anthocyanin of the same shade as the skin either in the centre or at the vascular ring, or irregularly placed and of varying degrees of intensity and frequency so that extreme types may be almost completely red or purple ; sometimes the flesh inside the vascular ring is pigmented and the cortex is unpigmented except for the outermost cell layers ; tuber eyes may be superficial (' fleet ') or to a greater degree sunken and indented so that the base of the eye is eventually completely enclosed ; shape of eye round to ovoid to very elongated ; ' brow ' hardly visible to completely overhanging or sometimes (rarely) marked as a long curved line on the smooth surface of the tuber ; eyes are often frequent but are generally infrequent and concentrated towards the distal end of the tuber (" rose end ").

Great differences in dormancy, sprout colour, cooking quality, starch, protein, Vitamin C and other qualities may also be noted according to variety and cultural conditions ; there is also a well-marked dormancy period, however, in contrast to the diploid cultivated species grouped around *S. phureja*. Tubers may be produced under long (15–18 hour) or short (8-12 hour) days according to subspecies, or developed at any intermediate day length.

Stem : varying from short (*ca.* 20 cm.) to tall (1 metre or more) according to variety and environment, produced in large numbers (5–10 or more) or few (1–4), in section angular, thin and bent or thick and fleshy, from about 5–20 mm. thick according to variety ; stem wings decurrent from leaf bases, about 0·5–5 mm. wide (perhaps more?) straight edged or sinuate (' crisped ') ; stem pigment ranges from absent through pale purple or reddish reticulation or marbling to intense purple or red-purple ; internodes short (3 cm.) to longer (10 cm.) ; nodes slightly or considerably swollen.

Leaf: interruptedly imparipinnate (some basal ones occasionally simple), set at an angle to the stem varying from *ca.* 30–60°, the rhachis either quite straight or arched over to a greater or lesser degree ; lateral leaflet pairs (juga) varying from (1–)3–5(–8), decreasing in size from apex to base, though the penultimate jugum is occasionally the largest, generally ovate, ovate-lanceolate, elliptic, or even obovate, *approximately twice as long as broad* (from 1·4 to 2·4 times); terminal leaflet generally longer and wider than laterals, from subcordate or suborbicular to broad ovate, broad elliptic, obovate or even rhomboid ; all these above-mentioned ' primary ' leaflets apically acuminate, fairly sharply delimited at base, sometimes cuneate or sometimes subcordate, the laterals often oblique, with petiolules (' ansae ') from (0–)1–5(–10) mm. or even to 25 mm. (according to Bukasov) long, sometimes, especially when long, bearing acroscopic, basiscopic or semibasiscopic interjected leaflets ; interjected leaflets (' folioles ', or leaflets of second, third, fourth, etc., order) much smaller than upper laterals, very shortly petiolulate or sessile, varying from (0–)1–10(–50)-jugate per leaf, generally similar in shape to primary laterals though much smaller and often broader ; leaf surface medium glossy to dull, never as brilliant as that of *S. phureja*, slightly rugose, medium to dark green above, paler below, provided with sparse to frequent multicellular semiadpressed hairs mixed with paucicellular or unicellular ones ; semi-lunar or reniform semi-amplexicaul pseudostipular leaves generally present, actually the modified terminal leaflets of the first two leaves on supressed axillary branches.

Inflorescence: produced terminally but becoming lateral subsequently owing to sympodial growth continued by an axillary branch from the *penultimate* leaf; flowers varying in number from few (two or three) to many (20 or 30), produced on a series of two or more monochasial helicoid cymes, according to the number of dichotomous branchings of the apex of the peduncle.

Peduncle: generally once or sometimes twice or more branched above, ranging perhaps from 5–20 cm. in length below the forks and 5–10 cm. long above the first branching.

Pedicels: (10–) 20–35 (–40) mm. long, separated from each other (not tightly grouped together as in *S. commersonii*), with a well-marked joint or articulation (which is sometimes pigmented), nearly always in the middle third, i.e. from 1/3 to 2/3 length above the base (occasionally higher but very rarely lower); pubescence as for leaf but may be sparse above articulation.

Calyx: campanulate, with generally fairly regular lobes, not fused together to form bilabiate or trilabiate mouth; lobes generally more or less ovate or broad ovate with well-defined narrow acumens from 1–5 mm. long and often transparent margins; pubescence of sparse to moderately frequent multicellular and unicellular hairs and sparse minute stalked glands.

Corolla: rotate, from (2–) 2·5–3·5 (–4) cm. diam., the lobes well defined, about (8–) 12–22 mm. broad × 4–15 mm. long, including the triangular acumen, the length therefore about 1/3 to 3/4 of the width (generally about 1/2); acumen itself *ca.* (2–) 3–5 mm. long × 5–7 mm. broad; colour varying from pure white through shades of pale pink and mauve to deep magenta or deep violet; streaks in centre of petals (' star ', ' tongues ') varying from pale green, silvery, to deep violet or glossy black; in many varieties the whole centre region of the petals including the acumens is much paler than the rest, even white, and this is especially marked below; sometimes the acumens only are white.

Androecium: anthers (4–) 6–7 (–8·5) mm. long, × (1·75–) 2·5–3 mm. broad at the generally cordate base, narrower above, sometimes shrivelled, or aborted, arranged in a conical or ovoid tight or loose column round the style, varying from very pale greenish yellow to deep orange or even reddish, rarely with anthocyanin on inner surface; pollen fertility varying from 0 to 100 per cent according to variety; filaments fairly short and thick, from (0·7–) 1–1·25 (–1·5) mm. thick and (0·8–) 1·5–2·5 (–4) mm. long, generally white, but may be pale yellow in some varieties, glabrous, very occasionally finely pubescent.

Gynoecium: ovary ovoid or slightly ovato-conical, slightly 2-grooved; style generally straight but occasionally spirally twisted or S-shaped, (9·5–) 10–11 (–13) mm. long × (0·45–) 0·55–0·65 (–0·75) mm. thick, with minute papillae (' mamillae ') densely arranged on its lower 1/3 to 1/2; stigma generally somewhat larger than style apex, capitate to subconical or clavate, entire, grooved or occasionally 2 (or more)-lobed.

Berries: none or produced in varying quantities, up to 4 cm. diam. or perhaps more, ±globose but sometimes slightly pointed, at first green, streaked or splashed with purple in certain forms, turning pale brown when ripe and at this time somewhat aromatic.

Chromosome number: $2n=48$.

Can be induced to form hybrids with many wild and cultivated species under experimental conditions and probably hybridizes to some extent with those wild and primitive cultivated diploid and triploid species that are sympatric with it.

The description I have given above may be criticized on the grounds that it is wide enough to include nearly every species of wild and cultivated potato, since the range of size and number of parts of leaf and flower structures is so very extensive. This difficulty must always arise, when we attempt to define the specific limits of cultivated plants with many different varieties and which are probably occasionally hybridizing with other nearly related species in the same area. I have attempted to define the more typical dimensions of the various organs by enclosing the more exceptional cases in brackets. I have included the range of variation of this species both in Europe and in South America, but no doubt there must be several forms known to botanists and potato breeders which do not quite fit the above description, and I regard it as, to some extent, tentative at the present time.

When we come to consider the description of S. *tuberosum* in detail and to compare it with the various species of wild potatoes we shall see that it is a comparatively easy task to separate those placed in the taxononic series other than *Tuberosa*. In Table I, I have noted the most outstanding characteristics by which species in these series may be separated from the cultivated tetraploid potato, *S. tuberosum*.

It is a rather more difficult matter, however, to set down a series of characters by which *S. tuberosum* may be separated from other cultivated potato species and from its nearest wild relatives in Series *Tuberosa*.

Tuber characters may be used in general for distinguishing the wild from the cultivated plants. Thus the wild species possess generally small tubers, *always* with superficial eyes and *never* with any red pigment nor with any special distribution pattern of the anthocyanin pigmentation. If anthocyanin is developed it shows as an ill-defined flush of blue-purple that is not confined in any constant way to special regions. Similarly, the red anthocyanin (in reality a red-purple, as distinct from blue-purple) coloration so frequently found in cultivated sorts is never displayed in the wild species ; since the red/blue coloration appears to be controlled by a pair of genes, blue being dominant to red, we can see that the red recessive mutation may well have developed at a late stage in the history of the potato after it had been taken into cultivation. The only apparent exceptions to this rule are with *S. leptostigma* Juz. (now grouped under *S. tuberosum*) and a form kindly sent to me from the Neuquén region of S.W. Argentina by Sr. J. Diem. In these, the pink tubers are an indication, confirmed also by other evidence, that the plants in question are escapes from cultivation and are not primitively wild.

TABLE I.—Characters of outstanding importance which serve to distinguish species in the below-mentioned series from *S. tuberosum* L.

Series	Distinguishing characters
1. Juglandifolia	No stolons or tubers ; woody stem ; yellow flowers.
2. Etuberosa	No stolons or tubers ; articulation of pedicel very low.
3. Bulbocastana	Stellate corolla ; simple leaves.
4. Cardiophylla	Stellate corolla. Only diploid and triploid forms known.
5. Pinnatisecta	Stellate corolla. Only diploid forms known.
6. Commersoniana	Stellate corolla. Only diploid and triploid forms known.
7. Circaeifolia	Stellate corolla ; long conical berries.
8. Acaulia	Very short stem ; auricled leaflet bases ; generally no pedicel articulation ; corolla lobes *very* short.
9. Demissa	Corolla with short lobes and small acumens. No tetraploid species known.
10. Conicibaccata	Leaflets generally more than twice as long as broad ; berries conical.
11. Piurana	Leaf glabrous, shining, poorly dissected ; corolla large, with short lobes.
12. Longipedicellata	Corolla circular in outline with sharply delimited acumens.
13. Cuneoalata	Leaf rhachis with cuneate wings ; no interjected leaflets.
14. Polyadenia	Dense glandular pubescence over the whole plant. Only diploids.
15. Megistacroloba	Leaf lobed, not pinnate, with very large terminal leaflet ; high pedicel articulation ; corolla semi-stellate.

Certain tetraploid weed potatoes that, on account of their non-cultivated status, have been previously separated from *S. tuberosum* must now be united to it. These, including the species *S. herrerae* Juz. and *S. subandigena* Hawkes and certain weed varieties from various parts of the Andes (see p. 134) must now undoubtedly be classed with *S. tuberosum* in the wider sense and according to the limits set by the description I have just given. The tubers are, in these cases, either unpigmented or with purple pigment, and it is therefore only by a sum total of their vegetative and floral characteristics that they can be seen to belong to *S. tuberosum*.

A useful character which helps to separate *S. tuberosum* from most wild species in series *Tuberosa* is the fairly constant length/breadth ratio of the upper lateral leaflets in the well-developed leaves ; the ratio varies from about 1·4 to 2·4 but by far the greatest number of *S. tuberosum* varieties come fairly close to the value of 2 ; that is to say, the length is twice the breadth. Many varieties of diploid cultivated species such as *S. stenotomum* Juz. et Buk. possess a length/breadth ratio of 3, though this is not always so, and it certainly comes closer to 2 in the Central Peruvian varieties of that species.

The large flowers, thick style, thick filaments and anthers, and large stigma also aid in delimiting *S. tuberosum* from the diploid and triploid wild and weed species. By its regular calyx with well-delimited and relatively small acumens *S. tuberosum* may be distinguished from *S. phureja* Juz. et Buk. and *S. stenotomum* and their relatives, in which the calyx is often bilabiate and nearly always irregular. Finally, since all the wild species and nearly all the weed species in *Tuberosa* are diploids (with one or two triploids only), *Solanum tuberosum* may be distinguished by its chromosome number and the generally more vigorous habit and thicker and larger stems, leaves and flowers as compared with those of diploid species.

7. Subdivisions of *S. tuberosum*—Russian Views.

I have considered the type specimen and description of the cultivated tetraploid potato, and have gone on to establish what seem to me to be the specific limits and range of variation that should be allowed at the present day, having in mind the immense variation in commerical varieties and the vast amount of material now available for study in South America.

It will be of value to consider at this point the views of previous workers in this field on the delimitation of the species and on its subdivisions.

Little work was done from a taxonomic point of view on the cultivated potato* until the expeditions sent to South America by the government of the U.S.S.R. during the years 1925–1932. The botanists who took part in them, namely Professor N. I. Vavilov, Dr. S. M. Bukasov and Dr. S. W. Juzepczuk, made collections not only of potatoes but of other cultivated plants as well, which might be of value in new plant breeding projects. In their first publication on the cultivated potatoes of South America, Drs. Juzepczuk and Bukasov (1929) seek to show that the variation observed is sufficient to separate a number of species from the original *S. tuberosum*.

They consider that the cultivated potato originated from a number of different wild forms and that therefore *S. tuberosum* should be regarded as a ' collective species '. Arguing from the fact that the characters used by Bitter (1912, 1913, etc.) to distinguish wild species one from the other were, in the case of *S. tuberosum*, used to differentiate varieties only, they considered that *S. tuberosum* in its turn should be divided into several specific units similar in status to the wild species. They felt that it was harmful to use different standards for the wild plants on the one hand and the cultivated ones on the other. These authors then go on to refer to the work of Rybin (published later, in 1930 and 1933) in which were established, in addition to the forms with the common number of chromosomes (i.e. 48) many others with 24 or 36 somatic chromosomes and again others with 60. Drs. Juzepczuk and Bukasov therefore established as distinct species those forms that differed in chromosome number from the tetraploid potatoes, noting the presence in both wild and cultivated potatoes of a polyploid series with a basic chromosome number of 12.

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* It is worth noting here that the names *S. triferum* Schlechtd. (1841) and *S. cayeuxii* Berthault (1911) were given to cultivated potatoes from Peru and Colombia respectively. Nevertheless, the names are of little value since the former bears no diagnosis and the latter has no type specimen.

Having dealt with the non-tetraploid potatoes which they established as eleven distinct species they then turned their attention to the tetraploids ($2n=48$), similar in this respect to the potatoes of Europe. Tetraploid potatoes were found to occur over a very wide geographical range, from Mexico and Guatemala in the north, southwards through the mountains of Colombia, Ecuador, Peru, Bolivia and North Argentina, and also on the sea coast of southern Chile in the region of the Island of Chiloé. In a corollary to this paper the authors pointed out that the Chilean tetraploids were very similar in appearance to the European potatoes, and they assumed therefore that these latter had originally been derived from Chilean sources. These European and Chilean potatoes they named *Solanum tuberosum* L., *sensu strictiore*, whilst the remaining tetraploids from the Andes they considered as sufficiently distinct " to constitute another polymorphic species (evidently of different origin) " which they named *Solanum andigenum* Juz. et Buk.*

In 1930 Bukasov, in discussing the potatoes of Mexico, Guatemala and Colombia, elaborated on his original ideas of the separate origins of the Andean and Chilean tetraploids. He considered that the Mexican and Guatemalan cultivated potatoes (which were all tetraploids) should be grouped under *S. andigena* on the basis of their morphology and photoperiodic response. He expresses some doubt, however, as to the antiquity of potato cultivation in those countries, since there are no references in the immediate post-conquest literature to this plant. It is possible, therefore, that the potato was cultivated either just before or at some time after the conquest, the basic material having been derived from Andean sources.

In his monographic study of the potatoes of South America (1933) Bukasov re-emphasizes the differences between his *S. andigena* on the one hand and *S. tuberosum* (*sensu stricto*) from Chile on the other. He considers that the European potatoes should be designated as *S. tuberosum* var. *europaeum* (typified by the variety ' Up-to-date '), since they differ, according to him, in certain respects from the Chilean potatoes, although a group of these latter are considered as of European origin (vars. *obliquum* and *roseum*).

On the whole he does not seem very convinced of the legitimacy of var. *europaeum*, since he follows a survey of the diagnostic characters by stating that " the concept of v. *europaeum* does not seem very definite but is rather hypothetical, particularly as the range of variation of the thousands of cultivated varieties has not been studied. Perhaps some clarity could be achieved if not all cultivated varieties were grouped under v. *europaeum* but only those that are most removed from the Chileans ".

When a writer states that of two botanical varieties, each has forms typical of the other, and that to distinguish them more clearly one should exclude these divergent forms, the reader may be forgiven for wondering whether there is any concrete reality in such a classification, and for entertaining doubts as to its validity.

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* Should be ' *S. andigena* ' according to Index Kewensis, Suppl. IX and XI (1947, 1953) ; I shall therefore use the revised Kew orthography from now on in the present work.

With regard to the classification of varieties within *S. andigena* Bukasov considers it possible to pick out seven main groups according to their salient morphological features and their geographical distribution, namely :

I. Colombian group.
II. Ecuadorean group.
III. Central Peruvian group.
IV. South Peruvian group.
V. Bolivian group.
VI. Argentine group.
VII. Mexican group.

Of these groups of forms he regards the Central Peruvian (Group III) forms as typical for the whole species. The *S. tuberosum* forms from Chile he regards as much less variable as compared with the range of diversity exhibited by *S. andigena*. Each ' species ' is presumed to have had a separate origin from wild species in its particular region, the wild progenitors of *S. tuberosum* being suggested as *S. leptostigma* and *S. fonckii*, whilst *S. herrerae* is considered as one of the ancestral types of *S. andigena*. Bukasov, further, mentions the work of Razumov (1931) in establishing that the Chilean varieties of *S. tuberosum* are able to form tubers in the long summer days of high latitudes, whilst those of *S. andigena* are adapted to the short 12-hour day-length of the tropics. This is adduced as further evidence that the Chilean *S. tuberosum* was the only ' species ' to gain widespread cultivation in Europe, where the day-length is approximately the same as in Chile. Nevertheless, he is still a little doubtful (p. 156) as to whether any commercial varieties might not have been obtained as hybrids from crosses between the two species. He quotes experiments by Nesterovich, Vesselovsky and others which demonstrate that in the F_1 hybrids of these two species many types are obtained free from the negative photoperiodic response of *S. andigena*, and he considers that short-day response is not therefore a dominant character*.

Later (1937) Bukasov lists the differences between his two cultivated tetraploids in some detail as follows :

" 1. *S. tuberosum* sensu stricto

Now comprises 48 chromosome forms of Chilean origin. Characteristics are as follows : Typical habit which consists in shorter internodes, more nearly horizontally disposed leaf, lesser dissection of leaf particularly in respect to size of segments. All this gives the impression of lower growth and a more bushy leafy plant. Pedicel above the articulation is often thickened and less clearly demarked from the calyx. The stamen filaments are often thicker and not infrequently yellowish and the style often thicker and often slightly spiral. The pollen is often sterile whilst tuber formation is good both in long and short day ".

" 2. *S. andigena*. This species in certain characters overlaps with *S. tuberosum* and this fact therefore makes difficult the differentiation between the two species. The fact is apparently explained by the circumstance that both species are of polyphyletic origin and will ultimately have to be divided into several species. The complex group of forms which at present constitutes *S. andigena* is geographically and physiologically quite distinct from *S. tuberosum*. The former are all mountain forms at a height of not less than 1–2000 metres. In long-day conditions they form no tubers. The habit is less leafy in consequence of the longer internodes, in view of the greater dissection of the leaves and smaller segments, and often the acuteness of the angle the leaves make with the stem. The filaments and style are thin. The pollen is with few exceptions fertile and the majority of forms produce berries ".

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*This is not substantiated by Hackbarth (1935), Salaman (1937) and others, who consider it to be on the whole dominant but to be due to the action of a large number of genes.

To sum up the view-point of the Russian scientists, then, we have two tetraploid cultivated potato species each derived separately from different wild ancestors, in different regions of South America and with different photoperiodic responses in respect of tuber formation. Nevertheless, we are told that they hybridize easily with no loss of fertility and that in their range of variability they overlap quite considerably. From the morphological similarity and similar photoperiodic response Bukasov and Juzepczuk suggest that the Chilean potatoes were the original source for the European sorts and hence should be known as *S. tuberosum* (*sensu stricto*), the Andean tetraploids being distinct enough to be given species status as *S. andigena*.

8. CRITICISMS OF THE RUSSIAN VIEWS BY SALAMAN AND HAWKES.

The whole fabric of the Russian thesis on the origin and inter-relationships of the tetraploid cultivated potatoes has been criticized by Salaman and by the present writer in a series of communications, the relevant portions of which we shall summarize below :

In 1937 Salaman criticized on historical grounds the view that the European potato came from Chile. Having obtained evidence that crops of potatoes were being grown in Spain at about 1570 he points out that the portion of Chile where the potato was then grown by the Araucanian Indians had not at that time been subdued by the Spaniards. Furthermore, no journey from Chile was made to Europe via the Straits of Magellan until 1579. The journey from Chile, supposing for the sake of argument that a tuber was indeed collected from that region, would need to have been made in several stages, involving transhipment in Lima, Panamá and Nombre de Dios. Thus it would have taken at least a year for the precious tuber to arrive in Spain and be planted in the following spring. There seem to be too many virtual impossibilities involved in the process for it to have happened. However, potatoes might have been brought down from the Andes to the Pacific ports of Lima, Payta, Tumbez or Buenaventura, or even possibly from Bogotá to Cartagena on the north coast of South America. Every ship that sailed to Spain stopped at Cartagena, and a regular trade route to the potato-growing regions of the interior had been opened up by 1549. It thus seems much more likely that it was the Andean potatoes that were the first to be brought to Europe when we consider the problem from the purely historical point of view.

When considered from the botanical aspect Salaman points out that the differences between the two species are only of value when taken as a whole or when extreme or 'typical' examples from each group are considered. If it is considered that there might be a linkage between the long-day habit and the broader leaflet typical of *S. tuberosum* then it is not surprising that during the centuries the breeder might have unconsciously selected from the original Andean sorts something resembling the Chilean potato which grows under conditions very similar to those of Europe. Breeding work has shown, furthermore, that the short-day photoperiodic response is not absolute, and that more long-day adapted plants may be selected from the progeny of short-day parental types. He further points out that the tubers depicted by Clusius, Bauhin and others are very much closer to those of Andean potatoes in their irregular shape and deep eyes than to those of the present-day European potatoes. Similarly, with the leaf characters and the high fertility of the early European and Andean potatoes on the one hand, as contrasted with the present-day European and Chilean potatoes on the other.

Salaman appends a summary in tabular form of the differences between the two S. American tetraploid 'species' and points out that there is no character in either of the two 'species' that could not be mirrored by a similar variation in the British domestic varieties. From this he concludes that the Russian thesis is completely unfounded, and that not only was the European potato brought from the Andes in the first place but that the tetraploid potato in South America is all one species, presumably the Andean one.

Hawkes (1944) pointed out the nomenclatural difficulty that arises if we consider that the early European potatoes came from the Andes ; according to the law of priority the name *S. tuberosum*, first given by C. Bauhin and adopted by Linnaeus, should then be used for the species which the Russians called *S. andigena*. However, since this latter name had become so well known it was considered better to leave it for the time and " to regard *S. tuberosum* (*sensu latiore*) as a collective species which includes the two sub- or micro-species *S. andigena* and *S. tuberosum* (*sensu stricto*) from the two geographical regions of the Andes and Chile respectively ". It was also felt that the name *S. tuberosum* should be retained for our domestic varieties, realizing that they were probably formed both from Andean and Chilean progenitors, and it was suggested that as the Chilean potatoes probably had no better claim to the name *S. tuberosum* than the Andean ones (in fact probably not such a good one) these might be called *S. chilotanum**.

In a later part of the same work, it was considered highly probable that the tetraploid complex originated in the Andes (Cuzco-Lake Titicaca region of South Peru and North Bolivia) and that the better yielding varieties spread out north and south at a slightly quicker rate than the poorer sorts, since this natural process is evident at the present day. The northern spread was stopped in Colombia by the low ground of the Panamá Isthmus. In Colombia many high-yielding varieties are to be found. The southern spread was halted in Chile, where the photoperiodic reaction of the potato became modified by the new day-length conditions. These Chilean forms were separated from their sources in Peru-Bolivia by the Atacama desert and the Andean Cordillera of N. Chile, and in the distinct latitudinal belt of South Chile eventually evolved into a new species referred to in that publication as *S. tuberosum sensu stricto*.

It is further pointed out as evidence for the single origin of the cultivated tetraploids that, since tetraploids are derived originally from diploid species, we should expect to find the diploid ancestors of the Chilean potato in the same region if the Russians' thesis were correct. This is *not* the case, however, since only the triploid (and morphologically distinct) *S. maglia* and the tetraploid *S. leptostigma*, *S. fonckii* and *S. molinae* occur in South Chile, whilst there are no diploid wild or cultivated potatoes within thousands of miles of this region. In Peru and Bolivia, however, there are hundreds of different forms of wild and cultivated diploid potatoes, which coincide in their distribution area and are morphologically very close to the cultivated tetraploids known to the Russians as *S. andigena*. It is therefore suggested that the tetraploid complex spread to Chile after the beginnings of agriculture and that this spread was largely dependent upon man's migrations, though evidently in the very remote past. The related tetraploid species *S. leptostigma*, *S. molinae* and *S. fonckii are* probably to be regarded as escapes from cultivation, an explanation further borne out by the red tuber pigmentation, which, as we have seen, is everywhere else confined to cultivated potato varieties.

Commenting finally on the Andean origin of the European potato, Hawkes points out that the potato was grown first in Spain and Italy at a latitude of 36°–45° N. whilst the latitude of Leningrad where the Russians grew it is 60° N. It is therefore likely that the short-day reaction of *S. andigena* may not have depressed its yield so much in those countries as it did in Leningrad and that probably quite good crops were obtained right from the beginning. When *S. andigena* was grown in New Zealand at the same latitude south of the equator the yields obtained were remarkably good. Thus the Andean potatoes were changed by artificial selection in Europe into a type similar to the Chilean ones in a matter of a few centuries, though the process in South America may have taken several thousands of years.

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* This name was not legitimized by a Latin description and its use for a variety of reasons has been discontinued.

In 1946 also, Salaman further attacked the Russian hypothesis of the distinctness of the two ' species ' S. *andigena* and S. *tuberosum* (*sensu stricto*) by studying in detail the leaves of the specimens brought back by the present writer from the South American Andes and comparing them with those of British domestic varieties. He concluded this work by stating that " not only is there no intrinsic difficulty in deriving our European potato from S. *andigena*, but there exist today and presumably did 350 years ago, varieties of potato in the northern parts of the distribution area of S. *andigena* [i.e. Colombia] which are, in the character of their leaf and the habit of their growth, similar to those now growing in Europe, and that in respect to their reaction to length of day as it affects stolon and tuber formation the majority of them behaved as did the earliest introductions of which we have records ". His considered view is therefore that the European potato almost certainly came from Colombia.

In 1954 Salaman augmented his views on the origin of the European potato by comparing the Andean and domestic forms with a series of Chilean varieties sent to England by Dr. K. O. Müller. From an analysis of the leaf types he concluded that the Chilean varieties studied were :

> " for the most part, straightforward examples of the species S. *andigena* which we have come to know so well in the north of South America. There would appear to be no reason based on morphology why we should look to Chile rather than the former [i.e. Colombia] for the original home of the European potato ".

A comparison of the leaves of Colombian and Chilean potatoes made in the present communication (see Table IV, p. 124 and fig. 5, p. 126) using different criteria from Salaman also reveals close similarities ; nevertheless, it should be reaffirmed that these two groups differ markedly in habit and photoperiodic response (see Table III, p. 122).

Salaman's thesis that " the domestic potato of Europe, though given the specific name of S. *tuberosum* is in fact a variety of the species S. *andigena* " cannot be maintained, however, in view of nomenclatural difficulties (see pp. 120). Nevertheless, all evidence points to the fact that these two taxa are conspecific, and that their separation as two distinct species cannot be maintained—a point that Salaman rightly stresses.

An additional piece of evidence for the Andean provenance of our European potatoes was brought forward by Salaman and Hawkes in 1949 when, by a series of photographs of old herbarium specimens of early 17th and 18th century potatoes, it was shown that certain of these were wholly like S. *andigena* in their general morphological aspect. The specimen which Caspar Bauhin himself made in about 1620 or perhaps earlier (see Pl. 3) is pure S. *andigena* in its habit, flower and leaf dissection, as also is that of Sébastien Vaillant in 1720, a century later. That of Linnaeus, however, as we shall see below, is not of this type. It seems proved, therefore, beyond reasonable doubt, that the first potatoes introduced into Europe were Andean ones and that later on, during the course of one or two centuries, and at any rate by 1753, the S. *andigena* forms were converted by selection under European conditions into what we now know as S. *tuberosum*.

9. The Composition of European Potatoes.

Although there seems little doubt that the *first* European potatoes came from the Andes, it is possible that other varieties might have been brought from Chile at a later date. If this were so, then our modern potato varieties would have originated from both Andean and Chilean sources. Perhaps even the varieties known to Linnaeus in 1753 were derived, in part at least, from Chilean progenitors.

Unfortunately, here again, as in so much of the history of the potato, the evidence is fragmentary and rests on insufficiently sound foundations. We have no indication of potato introductions from S. America in the 17th century and only very vague references to the American origin of the variety Yam in the 18th century. Bukasov (1933) quotes Putsche as stating that the Yam variety of potato was brought to England by a sailor from Surinam in Dutch Guiana. Since no indigenous potatoes are grown within several thousand miles of that country it is probable that the account is without foundation. Salaman (1949) records the legend that a tuber of this variety was washed up on the shore of Northumberland and that it was planted in the Duke of Northumberland's London home at Sion Park. He also mentions the name Surinam as a synonym. In addition to this Bukasov (1933) wonders whether the word Surinam may not have been derived from a native name ' Surimana ' given to a triploid Andean potato species *Solanum chaucha*. Since the variety Yam is tetraploid the explanation given by Bukasov is inadmissible. On the whole, one cannot help wondering whether the variety Yam was not perhaps a natural seedling which was given this name owing to the similarity of its tubers with those of the true Yam (*Dioscorea*). Although, therefore, apart from the Yam legend there are no records or stories of the introduction of Chilean or Andean potatoes into Europe in the 17th and 18th centuries there is of course no reason to exclude the possibility of the introductions of specimens which went unrecorded in the literature.

The first recorded introduction was that of Goodrich in America in 1851, who obtained a small quantity of potato tubers from the American consul in Panamá. Among these was a variety which, from its appearance and presumed place of origin, was designated Rough Purple Chili. From it were produced, in successive generations (from natural berries, probably produced by self-pollination) the varieties Garnet Chili, Early Rose and Beauty of Hebron.

Early Rose has proved of extreme importance in the history of the European potato since it gave rise to some 300 varieties, many of which are in use at the present day. As its name implies, it was an early potato, and gave rise through various generations to nearly all our first and second early modern varieties. The variety Daber is also said to be of South American origin and to have been introduced in about 1830, though no further details are known to me. It gave rise to many well-known continental varieties including the very well-known President.

Although Bukasov (1933) considered the variety Rough Purple Chili to be indeed of Chilean origin, Salaman (1946) denied this origin for both Rough Purple Chili and Daber, though the evidence for his statement was not given. The present writer is not in agreement with Salaman on this point, since it seems much more probable that both these potato varieties were obtained from Chilean sources.

We are told that the American Consul obtained tubers of Rough Purple Chili from the market of Panamá. Potatoes are not grown in the tropical lowlands of the Panamá Isthmus, but in view of the fact that Panamá City lies on the Pacific side of the Isthmus it would be easy enough for Chilean potatoes to be shipped up the coast from Valdivia or Valparaiso to Panamá, with no transhipment. Consider, on the other hand, the difficulties involved in conveying potatoes from the Andean region of Colombia to Panamá in 1851. Although Panamá was indeed part of Colombia in those days there was no direct land connection between Panamá and the potato-growing hinterland. Tubers might have got to Cartagena, but then would have had to be shipped to Nombre de Dios and transported on mule back over the Isthmus to Panamá.

To take potatoes from Bogotá to Panamá via Buenaventura would have been an even more hazardous task. Peruvian sorts could, however, have been transported there by sea with greater ease. If the varieties had been grown for one or two years in Panamá (and they were bought in the open market, presumably) then only Chilean and *not* Andean potatoes would have given any sort of yield. The writer has pointed out (1951, Dodds & Hawkes, 1952) the curious fact that in the tropics at altitudes of less than 1500 m. (5000 ft.) only long-day adapted potatoes can be grown (see later, pp. 127–133).

Another very interesting pointer to the probable Chilean origin of Rough Purple Chili is that the varieties produced from it and from Garnet Chili and Early Rose were very much earlier in their maturity than anything that had been known previously ; and both Early Rose and Beauty of Hebron are in the ' first early ' class. It seems to the present writer much more reasonable to suppose that good early-maturing varieties would have been produced in two generations of selfing from a stock *already adapted* to mature under long-day conditions in Chile, rather than to suppose that this result was obtained from Andean short-day plants which in Europe mature *very late*, in October and November, when the natural day-length becomes short enough for them. Although it is true that the extreme short-day reaction can be removed by breeding and selection, it seems highly unlikely that this could have been accomplished so successfully in two generations when we remember that photoperiodic response is almost certainly polygenically controlled.

The fact that Rough Purple Chili and its immediate progeny, together with the varieties bred from them, became so popular and have contributed so greatly to our newer varieties seems to me to be very strong evidence for the Chilean origin of this introduction. Not only this. The evidence points to the fact that this was the *first* introduction into Europe of Chilean potatoes, which had already become adapted to the day-length of temperate latitudes after many thousands of years under similar photoperiodic conditions. Had earlier introductions from Chile been made it seems that the importance of Early Rose as the progenitor of numerous first early varieties would not have been so great.

In the 20th century, with the phase of modern plant breeding, genes for resistance to disease have also been inserted into the new varieties from wild species such as *Solanum demissum* Lindl. and others. This, however, is a controlled process, and does not affect the present argument.

We can, therefore, with some justification modify our statement as to the origin of the European potatoes, to the effect that although they were derived at first purely from Andean sources, later, in the mid-19th century, there is strong evidence for believing that Chilean potatoes were crossed with them also.

Thus our modern varieties almost certainly possess a hereditary composition derived from both the Andean and the Chilean tetraploid complexes, a fact that has no doubt added greatly to their plasticity and variability.

10. Evidence from Hybridization Experiments as to the Conspecific Nature of Certain Tetraploid Forms.

We have seen that the Andean and Chilean races of the tetraploid potato differ from each other only to a limited extent, and that all the evidence seems to point to the conclusion that they should be grouped together as one species, *S. tuberosum* L. It has also been suggested that certain tetraploid weed forms, many of which must be regarded as escapes, should be included in this species.

It will be of value here to give the results obtained by the present writer in experimental studies on the interrelationships between species in the tuber-bearing section of the genus, so as to reinforce the views obtained from morphological studies.

Harland (1933, 1936) and Stephens (1950) have shown, in a study of the interrelationships of cotton species that many apparently ' good ' species form, when crossed together, perfectly viable and fertile F_1 hybrids. When these F_1 hybrids are selfed or sister plants crossed, the F_2 so produced, contains a large number of ' unthrifty ' or aberrant plants. Harland explained this by postulating species evolution by multiple gene substitution, whilst Stephens favoured the hypothesis of ' cryptic structural differentation ' of the chromosomes. Whatever the explanation, it would seem that the chromosomes of the two species are still sufficiently undifferentiated for them to pair quite regularly at meiosis, but that random segregation of chromosomes or parts of them with different genes controlling growth and general viability results, in the F_2 generation, in a high proportion of plants which are not able to survive. The facts have shown quite clearly that F_2 hybrids of varieties *within* a species are quite healthy, viable and fertile, whilst this is not the case when two " good " and well-differentiated species are hybridized together.

Several workers with *Solanum* species other than *S. tuberosum* have obtained results that fit in with this view (e.g. Propach (1940), Koopmans (1951), Bains (1951)). The results of the present writer on the tetraploid complex are briefly summarized in Table II.

TABLE II.—F_1 and F_2 generations of hybrids between various ' species ' now classed under *S. tuberosum* L.

Parents	F_1 (in 1952)		F_2 (in 1953)	
	Family number	Uniformity	Family number	Uniformity
S. andigena (2184)[1] × *S. leptostigma* (2128)	H.7	Very uniform growth. Some variation in flower colour.	H. 154	All plants uniform and thrifty. Some variation in flower colour.
S. subandigena (161·3) × *S. andigena* (1523b)	H. 11	Very uniform.	H. 157 H. 158	All plants very uniform and thrifty. Ditto.

[1] Numbers in brackets refer to the Commonwealth Potato Collection number.

It will be seen that in the F_2 families raised from crosses between ' *S. andigena* ' (from Peru) and ' *S. leptostigma* ' (from Chiloé, Chile), and between ' *S. subandigena* ' (from Bolivia) and ' *S. andigena* ' (from Peru), the F_2 families are composed of uniform thrifty plants. This may be contrasted with wide crosses made between species such as *S. goniocalyx* × *S. infundibuliforme* where the F_2 is extremely variable, consisting of a large number of plants that do not grow beyond the seedling stage.*

Thus we have from these crosses additional evidence for the conspecific status of the tetraploids which I have placed under *S. tuberosum*. Added to this is the fact, mentioned by Bukasov and other Russian breeders, that *S. tuberosum* (from Chile) and *S. andigena*, form perfectly viable hybrids. Unfortunately, I possess no living material of *S. herrerae* or *S. molinae*, and thus the experimental method cannot be used with these species at present. On the basis of the above-mentioned results, and other similar ones with the diploid cultivated and weed species (to be published later) there seems little doubt that

* A cross between the tetraploid Bolivian weed species *S. sucrense* Hawkes and *S. andigena* showed about 50 per cent unviable types in one F_2 family. This may therefore be specifically distinct, though the evidence needs further verification.

S. herrerae and *S. molinae* should be included under *S. tuberosum*. Further evidence in support of this hypothesis has recently been obtained by Gottschalk and Peters (1954). These workers studied the configuration of the macrochromomeres in the heterochromatic regions of the chromosomes at pachytene in a number of species, including *S. tuberosum* and *S. andigena*. The results indicated that these two ' species ' possessed identical chromosome sets as judged by the similarity of the heterochromatic segments, and therefore on this evidence also they could be regarded as conspecific. Furthermore, each haploid set consisted of pairs of identical chromosomes, thus giving further indications of the autopolyploid nature of *S. tuberosum*.

11. THE TAXONOMIC STATUS OF THE CHILEAN, ANDEAN AND EUROPEAN VARIETIES OF *S. TUBEROSUM*.

We are now in a position to consider how the nomenclatural position of *S. tuberosum* and its subdivisions is affected by the facts already established in the foregoing sections of the present work.

We have seen that *S. tuberosum* may be considered as a large complex and polymorphic tetraploid species, cultivated primitively in South America and later brought to Europe. The Andean forms of this species, grouped by previous authors as *S. andigena*, and adapted in their growth and tuber-forming requirements to the high mountains of the tropics with a short 12-hour day-length, are not sufficiently distinct to be grouped as a separate species, but would, in my opinion, very well qualify for consideration as a subspecies. They are confined to certain geographical and altitudinal belts, and although overlapping in their range of variability with the European and Chilean *S. tuberosum*, differ from them in many respects, as I shall show later. These Andean forms probably represent the primitive stock of tetraploid potatoes, centred in Peru and Bolivia, which in prehistoric times were carried to the coastal regions of South Chile where the climate is very similar to that of the high Andes, but where the length of day is 15–17 hours during the growing season instead of 12 hours. Here they evolved into what seems to be a geographical subspecies (known to the Russians as *S. tuberosum sensu stricto*) differing in a not very well-defined aggregate of characters, but chiefly in habit and photoperiodic reaction from their Andean ancestors.

In a similar way, but much later, Andean potatoes were brought to Europe, where the temperature and day-length conditions were very similar to those of Chile. Here they evolved in the same way, though the process in Europe was largely accelerated by artificial selection, so producing a plexus of forms so similar to the Chilean ones that they apparently cannot be separated from them with any degree of certainty. It was these European forms, very distinct even in 1753 from their progenitor, subsp. *andigena*, that received the name *S. tuberosum*. Later, as we have seen, in the 19th century, potato introductions were made from Chile also, so that modern European stocks are composed of genetic material from both sources.

Now, if one were describing potato species anew, with no reference to earlier publications or laws of priority, it would be much more convenient to describe the Andean forms (*S. andigena*) as the typical subspecies (since they are more ancestral) and the European and Chilean ones as the non-typical subspecies. However, since we must adhere to the laws of priority in botanical nomenclature the name *tuberosum* must take precedence over that of *andigena* even at the subspecific level, and must be attached to the lectotype in Linnaeus' herbarium (see p. 106). The Chilean and later European forms, which agree with this specimen, must be grouped under subspecies *tuberosum*, whilst the Andean forms, previously classed as *S. andigena*, are now to be considered as *S. tuberosum* subsp. *andigena*.

An alternative proposal would have been to consider C. Bauhin's specimen and description as the nomenclatural type for the species *S. tuberosum*. The following three points seem to me to militate against this, however :

(1) Although Bauhin's herbarium specimen may definitely be assigned to subsp. *andigena* there is no unequivocal evidence that Linnaeus ever saw it, or any of the other 17th century material that I have already mentioned.

(2) The woodcuts of Bauhin and Clusius, although adequate to show the main features of *S. tuberosum*, are too stylized for us to be able to refer them with certainty to either of the subspecies.*

(3) If we called Bauhin's *andigena*-like potato subsp. *tuberosum*, then the European and Chilean subspecies would require another subspecific name. The transfer of the epithet *tuberosum* from one subspecies to the other would result in utter confusion, especially amongst potato breeders, cytologists and geneticists. Since it is the purpose of taxonomy to prevent confusion the alternative proposal mentioned above would, it seems to me, be very ill-advised.

With the present scheme on the other hand, we can demote *S. andigena* from species to subspecies without changing either the epithet or its connotation—a very profound advantage when we are dealing with a plant which is being continually referred to in works not directly concerned with taxonomy.

The reader may well ask, at this stage, whether indeed there is any objective reality between what I shall now call subspecies *andigena* and subspecies *tuberosum*. To anyone who has worked with them or seen them growing together under experimental conditions both in Europe and South America there can be no doubt whatsoever about the reality of the two subspecies in question. The main differences are, however, of photoperiodic response and habit, whilst leaf differences may be, and in fact often are, less pronounced. Salaman (1946, 1954) indeed showed that many of the subsp. *andigena* forms from Colombia were, in their leaf type very similar indeed to those of certain Chilean and European varieties.

The following table (Table III, p. 122)† gives the main differential characters by which the two subspecies may be separated.

Whilst it is true to say that there is a large amount of overlap between the two subspecies, nevertheless if we consider the sum total of characters it will not be so difficult to place any unknown plant into its appropriate subspecific group.

Features such as the pale corolla with white tips and central petal streaks, stamens not fully developed and often aborted, rather sterile pollen, bent or twisted style, and infrequent berries may be due to many generations of artificial selection in Europe and may not be typical of the subspecies *tuberosum* as a whole. The effect of breeding for high yield and lack of intense pigmentation, without at the same time selecting for high fertility, may have produced this effect, though the possibility must not be excluded that breeders have tended to reject fertile strains in the belief that abundance of flowers and berries militated against a good yield of tubers. We know insufficient about the Chilean potatoes as yet to be able to state whether these characters of poor flowering and partial sterility are typical of subsp. *tuberosum* as a whole.

I have attempted to arrive at a more objective analysis (see Table IV) of the most important characters used to differentiate the two subspecies by assigning to each character a numerical scale. Since most of the comparisons are made on herbarium specimens I have dealt with leaf characters only, and have taken only a few samples from each group of forms. With each character I have assigned a higher number to its more *andigena*-like expression (as typified by the Central Peruvian forms of that subspecies) and a lower count to its more *tuberosum*-like expression (as typified by Linnaeus' specimen). The scale used for each character is arbitrary, the range of figures decided upon having been selected in order to give approximately the correct weight and importance to one character as compared with another.

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* See legends to figs. 1 and 2, however.

† Based on Bukasov (1930, 1933), Salaman (1937, 1946), and on observations in the herbarium and in the field by the present writer.

TABLE III.—Main differences between *S. tuberosum* subsp. *tuberosum* and subsp. *andigena*.

	subsp. *tuberosum*	subsp. *andigena*
Habit	Lower, more bushy, leafy, and 'closed'.	Taller, more straggling, and 'open'.
Stem	Generally short, with rather shortened internodes chiefly below; generally few stems (1–4) produced from each tuber, thicker and more fleshy.	Generally more elongated, with lengthened internodes; generally many stems (5–10) produced from each tuber, thinner and less fleshy.
Leaves	Densely disposed, almost at right angles to stem, or the base inclined at angle of 45–60° from stem.	Widely spaced, at an acute angle of 30–45° to stem.
Rhachis	Generally arched.	Generally upright, suberect or erectly spreading.
Dissection	Less dissected, with fewer interjected leaflets.	More dissected, with numerous interjected leaflets.
Leaflets	Closely spaced, usually broader; length/breadth: 1·4–2, with shorter petiolules; laterals ovate, acuminate.	Widely spaced, usually narrower; length/breadth: 2–2·4, with longer petiolules; laterals ovate to obovate or elliptic, shortly acuminate.
Inflorescence	Few-flowered.	Many-flowered.
Pedicels	Generally thickened above and passing gradually into the calyx base.	Not thickened above and passing abruptly into the calyx base.
Calyx	Larger, with longer bristly hairs and more rounded base; with well-developed acumens.	Smaller, with shorter less bristly hairs and more angular base; with shorter acumens.
Corolla	Frequently white or pale coloured, often with white acumens and white or pale central petal streaks.	Generally darker coloured (though white forms occur), rarely with white acumens or central petal streaks.
Filaments	Thicker (0·85–1·5 mm.) and often yellowish.	Thinner (0·88–1·13 mm.), white.
Anthers	Often not fully developed, and if well-developed, long.	Well-developed, generally shorter.
Pollen	Often rather sterile.	Generally fertile.
Style	Often thick and S-shaped or spiral.	Thinner, straight.
Stigma	Very large.	Smaller.
Berries	Generally not frequent.	Generally very abundant.
Tubers	Formed best in long days (in short days at altitudes of from 1500 to 8000 ft. (500–2500 m.)).	Formed best in short days at altitudes of 9000 to 13,500 ft. (2700–4000 m.), but not at lower altitudes, or under long, 15–17-hour, day conditions.

Thus in columns 1 and 2 I have given values of 10 to the narrow leaf angle and straight rhachis, since these are very important features of Bukasov's Central Peruvian forms of *S. andigena*. Columns 3 and 4 deal with the number of pairs of leaflets, high in subsp. *andigena* and low in subsp. *tuberosum*. The length/breadth ratio, of the largest lateral leaflet, multiplied by 5 to give it a value roughly equivalent to that of the other characters, is placed in column 5, whilst the same is done for the leaf as a whole in column 8. In column 6 an attempt has been made to define numerically the fact that subsp. *andigena* often exhibits an obovate terminal leaflet, whilst that in subsp. *tuberosum* is ovate. Petiolule length is dealt with in column 7, that of *andigena* being in general longer than that of *tuberosum*. A differential feature that I have not attempted to convey in figures is the degree of acumination of the leaflets. This is always slightly more in subsp. *tuberosum* than in subsp. *andigena*, in many varieties of which it may indeed be absent.

The samples have been arranged into 4 groups, as follows :

(I). *Early European*—from 1620 to 1750. The measurements are taken from herbarium specimens, or photographs of these published in Salaman & Hawkes (1949). (See Bauhin's specimen, Pl. 3.)

(II) *Cultivated Chilean*. Numbers 8–10 are based on herbarium specimens made in Chile by Dr. A. Montaldo, whilst numbers 11–14 are derived from the more extreme values in 4 families of seedlings raised in Birmingham from Chilean seed kindly supplied by Dr. K. O. Müller.

(III) *Wild Chilean and Argentine*. These wild potatoes are probably all naturalized forms of Chilean cultivated potatoes, as I have already mentioned. Here are included the important collections of Darwin, made in the Choños Archipelago south of Chiloé ; of Fonck, in the Guaytecas Archipelago situated between the Choños and Chiloé ; of Illín, in the Chubut territory of S. Argentina ; and of Diem in the Nahuel-Huapi region of Neuquén, also in S. Argentina. There are also two specimens of tetraploid weed potatoes collected by Müller and by Montaldo in Valdivia province and in Chiloé respectively. In addition I have included here an analysis of the two weed ' species ' described by Juzepczuk, namely *S. leptostigma* and *S. molinae* (see Map, page 128).

(IV) *Cultivated Andean*. Two groups of specimens from the Andes (subsp. *andigena*) are included here, namely, some of Dr. C. Ochoa's Central Peruvian collections and some of my own made in Colombia. There is also one specimen from N. Argentina. I have not been able to include here an analysis of my Andean collections made in 1939, and in any case the Table would have been too long if they had been added.

On the basis of the data set out, the following conclusions may be drawn (see also fig. 5). The values for the leaf indices of the wild and cultivated Chilean potatoes are uniformly low, ranging from 24–35 and 21–42 respectively. They coincide with the value for the Linnean type (27) and also with the specimens of Sherard (29) and Burser (26).

The Central Peruvian sorts are completely outside the range of the Chilean in their leaf indices, the values ranging from 52–79.

The values for the early European potatoes are of great interest in that they overlap both Chilean and Central Peruvian ones. Bauhin's specimen comes definitely within the Central Peruvian range whilst those of Sherard, Burser and Linnaeus come within the Chilean. Thus in respect of leaf characters these early European potatoes range from one subspecies to the other. Unfortunately, I have no specimens of modern varieties to compare with these, but from descriptions given by Salaman (1926 and especially 1946) the leaf type is definitely in the lower, Chilean range, as follows : Lochar=25, Majestic=34, King Edward=26, President=26, Ulster Chieftain=27. The range of these varieties is from 25–34 and thus corresponds with both Linnaeus' type and the Chilean potatoes.

Of particular interest are the Colombian varieties, since they correspond in leaf characters very closely to the Chilean (see also Salaman, 1954), and extend up to, though do not overlap, the range for the Central Peruvian ones. Thus potatoes introduced into Europe from Colombia would approximate much more

TABLE IV.—Leaf indices

No.	Collector and reference	*Leaf angle to stem* 0 = more than 45° 5 = ±45° 10 = less than 45°	*Rhachis arched or straight* 0 = arched 5 = indeterminate 10 = straight	Number of pairs of primary leaflets	Number of pairs of interjected leaflets
		1	2	3	4
	I.—EARLY EUROPEAN				
1	C. Bauhin ; Basle ; 1620	10	10	6	11
2	J. Burser ; Uppsala ; 1620	0	0	4	3
3	J. Bobart, senior ; Shrewsbury ; 1676	5	5	5	4
4	S. Vaillant ; Paris ; *c.* 1700. (a)	10	10	5	12
5	,, ,, ,, (b)	5	10	4	7
6	Herb. Sherard ; *c.* 1700	0	0	4	3
7	C. Linnaeus ; *c.* 1750	0	0	4	2
	II.—CULTIVATED CHILEAN				
8	Montaldo No. 72. Chiloé	0	0	3	0
9	,, 71. Chiloé	5	0	3	1
10	,, 68. Chiloé	0	0	4	2
11	*Müller (1952) ; Chillán. " Chagua "	0	0	6	3
12	* ,, Chiloé —	0	0	6	12
13	* ,, nr. Chiloé. " Achao "	0	0	5	5
14	* ,, Llanquihué. " Frutillar "	0	0	7	10
	III.—WILD CHILEAN AND S. ARGENTINE				
15	Illin, 234. Argentina, Chubut	0	5	3	5
16	Fonck, 102^{c}. Chile, Guaytecas	0	0	4	3
17	Darwin, 194. Chile, Choños	0	5	4	2
18	Montaldo, 69. Chile, Chiloé	0	0	4	2
19	Müller (1952). Chile, Valdivia	0	0	2	0
20	Diem, 1997. Argentina, Neuquén	5	0	3	1
21	*S. leptostigma*	0	0	4	8
22	*S. molinae*	0	10	4	1
	IV.—CULTIVATED ANDEAN				
23	Ochoa, 7. Central Peru	10	10	6	5
24	,, 12. ,,	10	10	6	14
25	,, 35. ,,	10	10	4	2
26	,, 36. ,,	0	10	7	15
27	,, 40. ,,	10	10	7	21
28	Hawkes, 157. Colombia " Guata "	5	10	5	4
29	,, 171. ,, " Careta "	0	0	4	2
30	,, 172. ,, " Guata "	0	0	5	6
31	,, 173. ,, —	0	10	4	2
32	,, 335. ,, " Clara "	5	10	4	6
33	Hjerting, 258^{c}, Argentina. " Collareja "	5	10	5	5

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* These collections were sent in the form of seed. The figures given are for the more highly

of tetraploid potatoes.

Length/breadth × 5 of largest lateral leaflets	*Greatest width of terminal leaflet* 0=below centre; 2=at centre; 4=above centre	*Length of petiolule of penultimate leaflets* $0=$sessile, $1=\frac{1}{8}''$, $2=\frac{1}{4}''$, $3=\frac{3}{8}''$, $4=\frac{1}{2}''$, $5=>\frac{1}{2}''$	Length/breadth × 5 of complete leaf	TOTAL LEAF INDEX	RANGE	Notes
5	6	7	8	9	10	
10	4	3	13	67	26–69	Abundant flowers
9	0	2	8	26		,, ,,
10	2	1	11	43		Medium flowering
10	4	5	13	69		Abundant flowers
10	2	3	10	51		
10	2	2	8	29		
9	2	1	9	27		TYPE SPECIMEN
9	0	1	8	21	21–42	In Herb. J. G. H.
9	0	1	9	28		,, ,,
9	0	1	8	24		,, ,,
8	2	2	9	30		Grown at Birmingham
9	2	3	10	42		,, ,,
9	2	2	14	37		,, ,,
8	2	3	10	40		,, ,,
10	0	2	7	32	24–35	" *S. maglia* v. *chubutense* "
10	0	2	7	26		" *S. maglia* v. *guaytecarum* " [= *S. fonckii*
10	0	2	5	28		
8	0	1	11	26		
9	0	1	12	24		
10	0	0	10	29		
8	0	2	9	31		Calculated from description
9	0	2	9	35		,, ,,
8	4	1	11	55	52–79	In Herb. J. G. H.
10	2	3	13	68		,, ,,
10	4	1	11	52		,, ,,
8	2	3	10	55		,, ,,
11	4	2	14	79		,, ,,
10	4	1	11	50	25–50	,, ,,
8	2	1	8	25		Leaflets not acuminate
8	2	0	7	28		Slightly acuminate
10	0	0	10	36		In Herb. J. G. H.
10	2	1	11	49		,, ,,
11	4	3	10	53		,, ,,

dissected and *andigena*-like of three seedlings scored for these characteristics in each case.

closely to our subsp. *tuberosum* in their leaf characters. Most Colombian varieties have rather poor leaflet acumination and differ furthermore from the European ones in their abundant flowering, and adaptation to short-day length.

In this scheme I have not been able to indicate habit, flowering and photoperiodic response. In the latter character the Andean potatoes differ extremely from the Chilean and the modern European sorts.

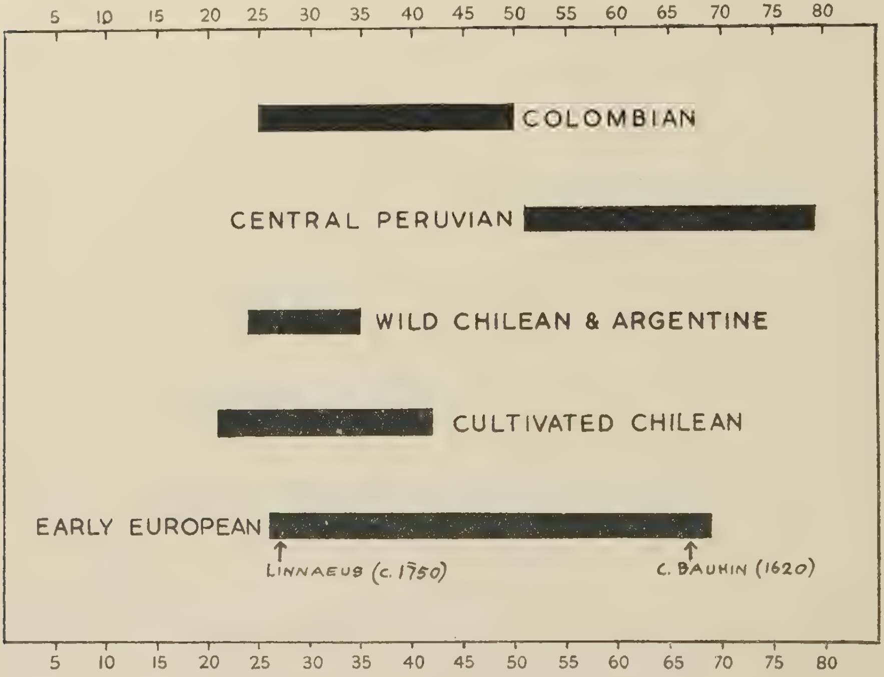

FIG. 5.—Leaf indices of tetraploid potatoes.
(For explanation, see text, p. 123.)

With the reservation that the foregoing results are based on a rather sparse number of samples in each group we can nevertheless state that leaf characters do, on the whole, reinforce other data in drawing at least a *subspecific* distinction between the Andean forms on the one hand and the Chilean and modern European (1750 onwards) forms on the other. I began this survey with the idea that it might be possible to distinguish the European from the Chilean potatoes, but the evidence available at the moment does not justify such a separation. If in the future it becomes necessary to separate the Chilean forms as a third subspecies, they might be named subsp. *chileanum*. That Bukasov also had grave doubts as to the advisibility of separating the European potatoes (' *S. tuberosum* var. *europaeum* ') from the Chilean ones (' *S. tuberosum sensu stricto* ') may be seen by reference to his monograph on the South American potatoes published in 1933, in which he says : " The concept of var. *europaeum* does not seem very definite but is rather hypothetical, particularly as the range of variation of the thousands of cultivated varieties has not been studied. Perhaps some clarity could be achieved if not all cultivated varieties were grouped under var. *europaeum*, but only those that are furthest removed from the Chileans ". Such methods as are outlined in the last sentence quoted seem to me to be highly questionable, and one can only conclude that either there is in fact no real difference between the two groups of forms, or that if it exists we have not yet discovered it.

12. DESCRIPTIONS AND DISTRIBUTION OF SUBSP. *TUBEROSUM*.

It now only remains to give descriptions for the two subspecies that I have established in the present work, together with a survey of their distribution :

S. TUBEROSUM L. subspecies *TUBEROSUM*.

S. tuberosum var. *chiloense* A. DC., *Arch. Sci. Phys. Nat.*, **15**, 437 (1886).

S. chiloense (A. DC.) Berthault, *Ann. Sci. Agron.*, Paris **28**, 179 (1911).

S. tuberosum var. *cultum* A. DC., *Arch. Sci. Phys. Nat.*, **15**, 437 (1886).

S. cultum (A. DC.) Bethault, *Ann. Sci. Agron.*, Paris **28**, 179 (1911).

S. tuberosum var. *sabini* A. DC. *pro parte, Arch. Sci. Phys. Nat.*, **15**, 437 (1886).

S. fonckii Phil. ex Reiche, *Fl. Chile*, **5**, 351 (1910) (*nomen nudum*).

S. sabini (A. DC.) Berthault *pro parte*, *Ann. Sci. Agron. Paris*, **28**, 179 (1911).

S. maglia Schlechtd. var. *guaytecarum* Bitter, in *Fedde, Repert. Sp. Nov.*, **12**, 2 (1913). (=*S. fonckii* Phil.).

S. maglia var. *chubutense* Bitter, in *Fedde, Repert. Sp. Nov.*, **12**, 452 (1913).

S. tuberosum L. *sensu stricto* Juzepczuk et Bukasov, *Trudy Vsesoyuzn. Syezda Genetike*, **3**, 609 (1929).

S. tuberosum var. *europaeum* Bukasov, Suppl. 47 *Bull. Appl. Bot. Genet. & Pl. Breed* (1930) (*nomen nudum*).

S. leptostigma Juzepczuk, *Bull. Acad. Sci. URSS.*, Sér. Biol., No. **2**, 310 (1937).

S. molinae Juzepczuk, *ibid.*, 308 (1937).

Includes forms with short bushy habit ; leaves arched, spreading, set at a wide angle to stem, broad, rather short, with medium to poor dissection, rather broad acuminate leaflets and short petiolules ; pedicels often thickened above ; corolla pale ; anthers often distorted ; filaments broad, often yellowish ; style often curved. (For detailed comparison see Table III.)

DISTRIBUTION (see Map).

(I) Cosmopolitan, but cannot generally be cultivated in the tropics from sea level† up to about 500 m., or above 2,500 m.

(II) Primitive cultivation area in the Araucanian region of South Chile at or near sea level, including provinces Chiloé*, Llanquihue*, Osorno*, Valdivia*, Cautín*, Malleco, Bio-Bio, Arauco, Concepción, Ñuble*, Linares, Maule, Talca*, Curicó*, Colchagua*, O'Higgins*, Santiago*, Valparaiso*, and Coquimbo*.

(Those provinces marked with an asterisk (*) produced a yield of 46,000 tons or more during the season 1949–50 according to Montaldo (1950).)

Although potatoes are cultivated at the present-day from Chiloé and Llanquihue (43° S.), northwards to Santiago and Valparaiso (33° S.) and in small quantities even farther north, the exact distribution of potato culture in pre-conquest days is not well known. According to Cooper (1946), potatoes were grown by the Mapuche and Huilliche tribes of Araucanian Indians who inhabited the region south of the River Bio-Bio (Provs. Bio-Bio, Cautín, Malleco, Valdivia, Osorno, Llanquihue and Chiloé) but little is known of the northern Picunche tribes, who were conquered by the Incas in about 1448–82 during the reign of Inca Tupac Yupanqui. Apparently no record exists as to whether these northern tribes cultivated the potato, but if they did, one can suspect that, from the Mediterranean climate, potato culture was on a very small scale.

(III) Weed and escaped forms of this subspecies have been recorded in both Chile (Provs. Chiloé, Valdivia) and S.W. Argentina (Gobs. Neuquén, Chubut (? also Rio Negro)) as follows :

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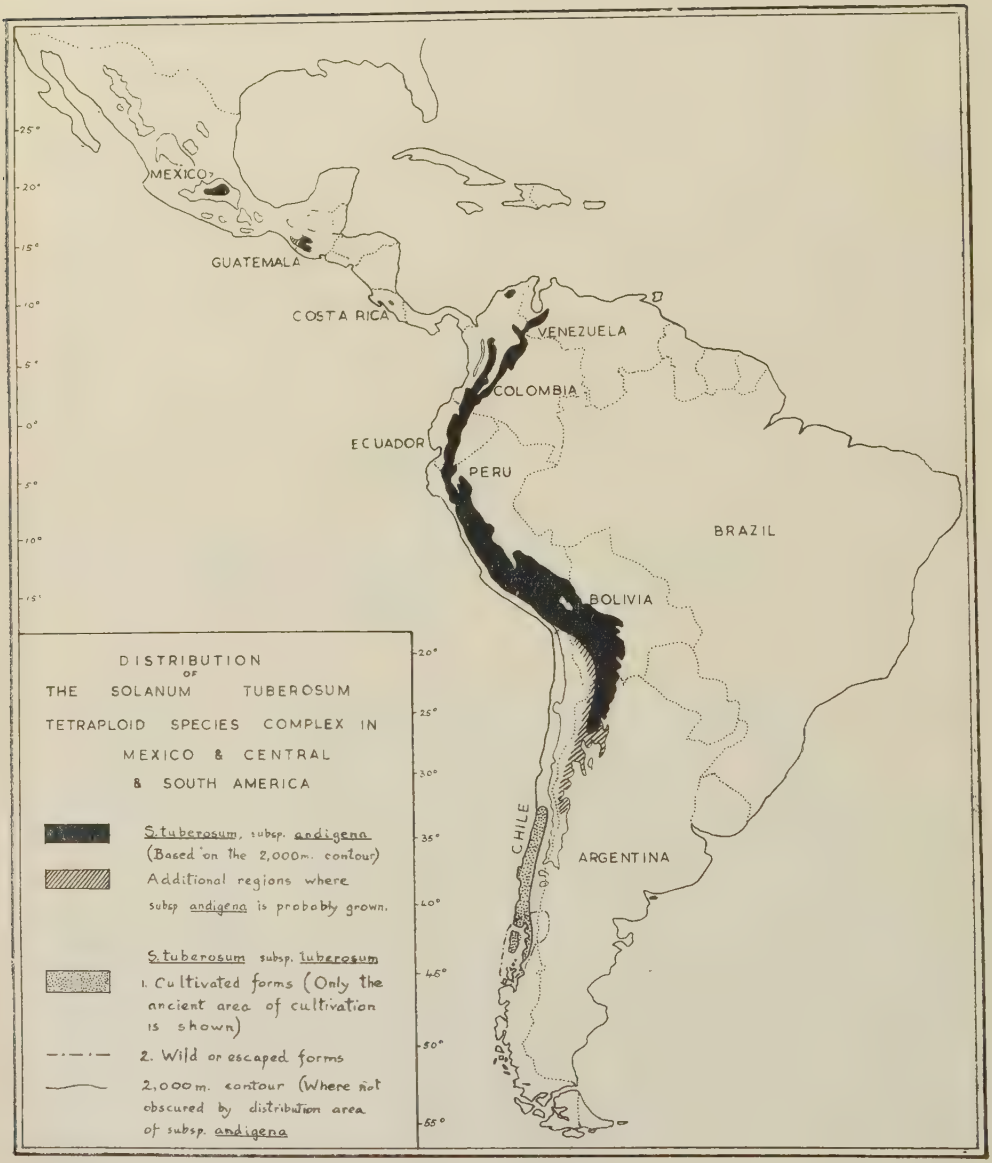
† Except in certain regions during the cool winter season.



DISTRIBUTION OF THE SOLANUM TUBEROSUM TETRAPLOID SPECIES COMPLEX IN MEXICO & CENTRAL & SOUTH AMERICA

S. tuberosum, subsp. andigena (Based on the 2,000m. contour)
Additional regions where subsp andigena is probably grown.
S. tuberosum subsp. tuberosum
1. Cultivated forms (Only the ancient area of cultivation is shown)
2. Wild or escaped forms
2,000m. contour (Where not obscured by distribution area of subsp. andigena
MEXICO
GUATEMALA
COSTA RICA
VENEZUELA
COLOMBIA
ECUADOR
PERU
BRAZIL
BOLIVIA
CHILE
ARGENTINA
25°
20°
15°
10°
5°
0°
5°
10°
15°
20°
25°
30°
35°
40°
45°
50°
55°

CHILE, *Island of Chiloé.*

(1) Cucao. Propagated by Junge in Piruquina, 6 Feb. 1932. *Junge* 276 (Isotype in Herb: L.). This collection was named by Juzepczuk as *S. leptostigma* Juz. (2) Near Cucao. Grown in a garden near the town of Castro. *Robert Christie* (as *S. molinae* Juz. Material not examined by me). (3) Dept. Castro, Cucao, shores of Lake Huillinco. In pastures, near *Hordeum, Lotus,* ferns and *Agrostis.* 4–5 March 1951. *A. Montaldo* 69 (Herb : J.G.H.). (4) Region of Cucao. Cultivated at Ancud, Puntia, from seeds of wild potato. 30 Jan. 1932. ' Papa negra '. *Macmillan & Erlanson* 94 (Herb : US). (5) Forests. Cultivated at Prov. Malleco, Angol, ' El Verjel ', from tubers collected by E. E.Reed. Corolla white. 27–28 Feb. 1925. *F.W. Pennell* 12850 (Herbs : F, GH, NY, US.). (6) ' *S. esculentum* ? var.' *Philippi,* (1862) (Herbs : G-Del, G-Boiss.). This is the specimen on which A. de Candolle based his var. *chiloense* (1886), raised to specific status by Berthault in 1911.

Prov. Valdivia : (7) Near La Unión. ' Tuber-bearing wild potato growing in wet locality on virgin soil '. 20th Jan. 1952. *Schuchardt.* (Herb. J.G.H.).

Guaytecas Archipelago : (8) Northern part, opposite the small island ; sandy beach. 6 March, 1857. *Fonck* 102c (Herbs : P (type for *S. maglia* Schlechtd. var. *guaytecarum* Bitt), W.). This is also stated to be the collection named by Philippi as *S. fonckii* Phil. (*nom. nud.*) *fide* photo in Herb. F, No. 33074 of the now destroyed Berlin sheet.

Choños Archipelago: (9) Dec. 1834. *C. Darwin* 194 *bis* (Herbs : CGE, K.). According to Darwin (1845) these potatoes " grow in great abundance on these islands on the sandy shelly soil near the sea beach. The tallest plant was four feet in height. The tubers were generally small, but I found one, of an oval shape, two inches in diameter : they resembled in every respect, and had the same smell as English potatoes ; but when boiled they shrunk much, and were watery and insipid, without any bitter taste. They are undoubtedly here indigenous : they grow as far south, according to Mr. Low, as lat. 50°, and are called Aquinas by the wild Indians of that part: the Chilotan Indians have a different name for them ". (10) Choños and Tres Montes. Wild. Jan. 1857. *Fonck* (Herb : P).

ARGENTINA : *Gobernación del Chubut.*

(11) Region of Rio Corcovado, between Bolsón* and Colonia. 1 Feb. 1901. *Illin* 234 (Herbs : BR, CORD, G-Del, HBG, SI). This was the type collection for Bitter's *S. maglia* Schlechtd. var. *chubutense* Bitt. (12) Lago Puelo. " Found wild and grown by some for eating. Corolla white, slightly tinted red-violet. Anthers yellow. Grown in the garden of the Facultad de Agronomía, Buenos Aires." Nov. 1926. *Millán* 577 (Herb : BA). (13) *Ibid. Millán* 592 (Herb : BA). (14) *Ibid. Millán* 1027 (Herb : BA). (15) *Ibid. Millán* 1028 (Herb : BA).

Gobernación del Neuquén : (16) Península Quetrihué, in damp shady wood. Alt. 800 m. 18 Jan. 1952. Young plants with very long and little buried stolons, with tubers. *José Diem.* 1997 (Herb : J.G.H.) (17) Península Quetrihué. High part of *Myrceugenella apiculata* wood. Alt. 820 m. Flower white, slightly rose-lilac. Alt. 0·3–1·2 m. Stolon 1·62 m. long, with tubers. Adult plant from a place with somewhat more light. *José Diem* 2050 (Herb : J.G.H.) (18) Bariloche, Los Arrayanes. Received 1 Oct. 1953. *Diem.* (Tuber Line H.5.) Tubers pink. 2n=48 (Herb, et hort : J.G.H.) (19) Península Quetrihué, 770 m. 16 Jan. 1951, Fl. viol. *H. Sleumer* 1520 p.pte. (with *S. brevidens* Phil.) (Herbs : LIL, J.G.H.).

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* Rio Corcovado is in Chile and Bolsón in the Gobernación del Rio Negro. However, the border is very close and in any case may have changed or been ill-defined when this plant was collected.

There seem to be two main groups of wild forms under the Chilean subsp. *tuberosum*, namely, those from the Argentine side of the Cordillera, typified by Bitter's *chubutense* (*Illin* 234), and those from the Chilean islands, typified by Bitter's *guaytecarum* (*Fonck* 102*c*). The former has much less disparity between the size of the terminal and lateral leaflets, than has the latter variety *guaytecarum*, where the terminals are very greatly enlarged. Darwin's sample, and possibly also *S. molinae* Juz., which I have not seen, come within var. *guaytecarum*. Living collections are particularly needed of these wild or escaped Chilian and Argentine potatoes and it would be of great interest to obtain samples from much farther south, where, according to Darwin (l.c.) and Fonck (collection data for No. 10 above) the wild forms of *S. tuberosum* are also to be found.

Bitter placed these two varieties with *S. maglia* erroneously, on the basis of leaf shape. They differ very significantly in the anthers which are well defined in *S. tuberosum* but which in *S. maglia* gradually pass into the filaments without any well-defined demarkation. This feature is to be seen in all forms of *S. maglia*, and is not only confined to the triploid variety from the region of Valparaiso, but is seen also in a diploid collection which I obtained from Mendoza in Argentina. *S. maglia* is a species that grows under much drier conditions farther north, whilst the rainfall of the Choños Archipelago is very high. Darwin (1845) expresses surprise that Professor Henslow should consider his collection from the south to be conspecific with *S. maglia* from Valparaiso, by saying : " It is remarkable that the same plant should be found on the sterile mountains of Central Chile, where a drop of rain does not fall for more than six months, and within the damp forests of these southern islands ". Despite this observation of Darwin and the characteristic differences in stamen form, both J. G. Baker (1884) and Bitter (1913) have erroneously persisted in classing the specimens from the Choños Archipelago as a variety of *S. maglia*.

We shall therefore transfer Bitter's names from *S. maglia* to *S. tuberosum* as follows :

S. TUBEROSUM var. *CHUBUTENSE* (Bitter) Hawkes, comb. nov.

S. maglia var. *chubutense* Bitter in *Fedde, Repert. Sp. Nov.* **12**, 452 (1913) (see fig. 6).

S. TUBEROSUM var. *GUAYTECARUM* (Bitter) Hawkes, comb. nov.

S. maglia Schlechtd., var. *guaytecarum* Bitter in *Fedde, Repert. Sp. Nov.* **12,** 2 (1913). *S. fonckii* Phil. ex Reiche, Fl. Chile, **5,** 351 (1910) (*nomen nudum*) (see fig. 7).

13. Description and Distribution of subsp. *andigena*.

S. TUBEROSUM subsp. *ANDIGENA* (JUZ. & BUK.) HAWKES, subsp. nov.

S. andigena Juzepczuk & Bukasov in *Trudy Vsesoyuzn. Syezda Genetike*, **3,** 609 (1929).

S. herrerae Juzepczuk in *Bull. Acad. Sci. URSS., Sér. Biol.*, No. **2,** 310 (1937).

S. subandigena Hawkes, Potato Collecting Exped. Mexico & S. Amer. : II Syst. Classif. Collect. *Imp. Bur. Pl. Breeding & Genet., Cambr.*, 53, 128 (1944).

Differs from *S. tuberosum* subsp. *tuberosum* in its tall ' open ' habit, with numerous elongated stems, suberect or erectly spreading straight leaves, set at a narrower angle to the stem, with many primary leaflets and often a large number (to 50) of interjected leaflets ; primary leaflets rather narrower than in subsp. *tuberosum* and less acuminate, with often very long petiolules ; pedicels not markedly swollen at the apex ; corolla generally intensely coloured or white ; anthers perfect ; filaments somewhat narrower than in subsp. *tuberosum*, white ; style straight. Forms tubers best under short days. (For detailed comparison see Table III.)

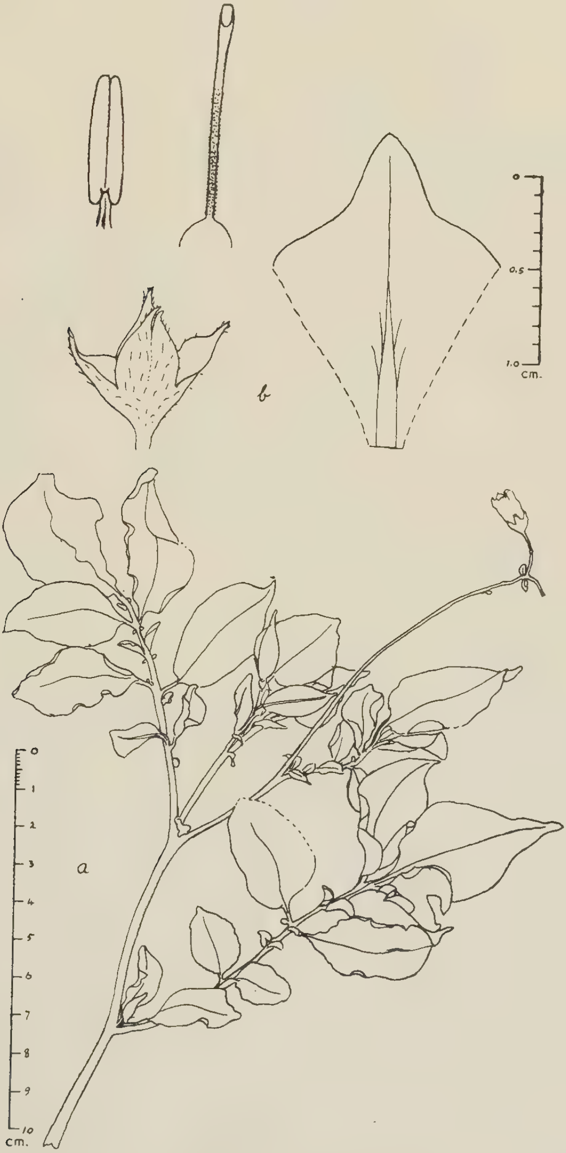

FIG. 6.—*Solanum tuberosum* L., subsp. *tuberosum*, var. *chubutense* (Bitter) Hawkes. S. Argentina, Gob. del Chubut. *Illin* 234. (*a*) Whole plant (Herb. G–Del). (*b*) Dissected flower (Herb. SI).

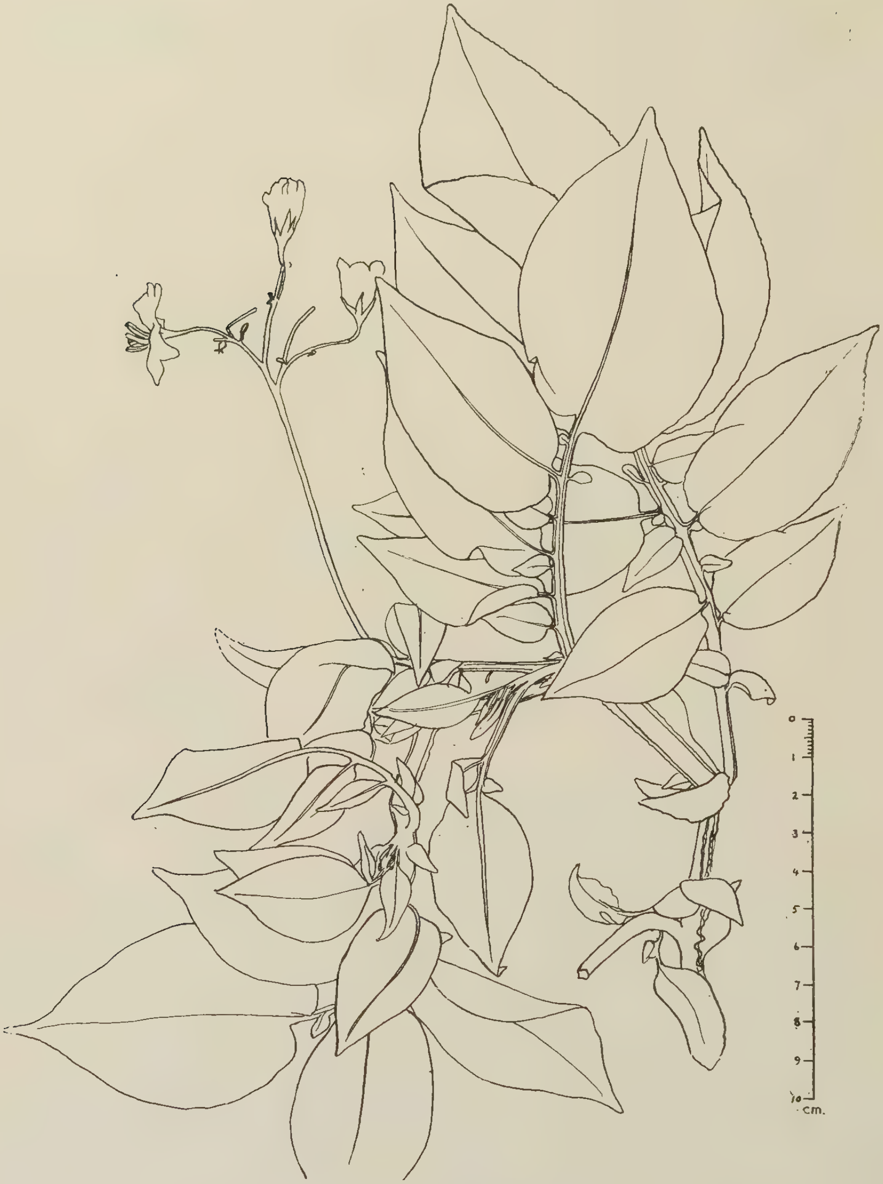

FIG. 7.—*Solanum tuberosum* L., subsp. *tuberosum*, var. *guaytecarum* (Bitter) Hawkes. S. Chile, Guaytecas Archipelago. *Fonck* 102*c*. (Herb. P.)

DISTRIBUTION.

(1) Cultivated in the mountainous regions of Mexico and Central and South America at altitudes of over 2000 m. (though sometimes, according to Bukasov, extending down to 1700 m.)*. Optimum growth conditions probably

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* Probably very rarely (J. G. H.)

between 2500 to 3500 m. or even higher. Recorded up to 4000 m. in Peru and Bolivia. In its latitude range it probably does not spread farther north than 20° N. or farther south than 33° S. Greatest concentration of forms between 10° N. and 23° S. Approximate range is as follows† (see also Map).

(i) *Mexico* : States of Mexico, Hidalgo, Distrito Federal, Tlaxcala, Puebla and Vera Cruz.

(ii) *Guatemala* : Departments of Amatitlan, Escuintla, Huehuetenango, Quezaltenango (Quiché, Santa Rosa, Totonicapán).

(iii) *Venezuela* : States of Mérida and Táchira.

(iv) *Colombia* : Departments of Antioquia, Boyacá*, Caldas, Cauca, Cundinamarca*, Huila, Magdalena, Nariño*, N. Santander, Santander, Tolima, Valle.

(Those marked with an asterisk produced over 48,000 tones in 1948 according to official Colombian Ministry of Agriculture reports.)

(v) *Ecuador* : Provinces of Azuay, Bolívar, Cañar, Carchi, Chimborazo, Imbabura, León, Loja, N.W. Napo-Pastaza, Pichincha, Tunguragua.

(vi) *Peru* : Departments of (Amazonas), Ancash*, Apurímac*, Arequipa*, Ayacucho*, Cajamarca, Cuzco*, Huancavelica, Huánuco, Junín*, Libertad, Lima*, Moquegua, (Piura), Puno*, Tacna.

(Those marked with an asterisk produced more than 45,000 tons in 1951 according to Peruvian official statistics.)

(vii) *Bolivia* : Departments of Chiquisaca, Cochabamba, La Paz, Oruro Potosí, Tarija.

(viii) *Chile* : Province Tarapacá, mountains behind Arica. (See Montaldo, 1951.)

(ix) *Argentina* : Provinces of Catamarca, Jujuy, (La Rioja), (Mendoza), Salta, (San Juan), Tucumán.

14. FURTHER NOTES ON THE DISTRIBUTION OF THE CULTIVATED FORMS OF SUBSP. *ANDIGENA*.

(1) *Mexico and Guatemala* : There is some doubt as to whether subsp. *andigena* is truly indigenous to Mexico and Guatemala, and its cultivation in regions other than Toluca and Orizaba is probably rather limited ; in these two regions, however, I have seen it cultivated in great profusion. It has also been recorded for Mt. Malinche, in Tlaxcala State (*Balls* 4875 *p.pte.*). Linden's specimen from Mt. Orizaba (Vera Cruz State) is of interest in that it was collected as long ago as 1838 (*J. Linden* 244. Herbs : FI, K.) ; subsp. *andigena* is certainly not a very recent introduction into Mexico, therefore. This subspecies probably always occurs in Mexico at altitudes of 2500 m. (8200 ft.) or more, and although many other records for potatoes exist it would be necessary to check over the specimens in order to make sure that they were of subsp. *andigena*. Commerical plantations of subsp. *tuberosum* are frequent in the Bajío region (±2000 m.) north of Mexico City and elsewhere ; the seed tubers for these are not indigenous, however, but are generally imported from Europe and N. America (U.S.A., Canada).

As to the exact distribution in Guatemala I rely on data from Bukasov (1930) and on certain lines sent to Cambridge by Dr. S. G. Stephens in 1947. Much more collecting in that country is needed before we are certain of the distribution areas of potato species there.

(2) *Colombia :* Potato cultivation is mainly concentrated in the region of Boyacá and Cundinamarca on the one hand (Cordillera Oriental) and in Dept. Nariño (near the Ecuadorean border) on the other. The tetraploid potatoes of

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† Doubtful records, or where there is some uncertainty or lack of botanical evidence, are placed in parentheses.

the Sierra Nevada de Santa Marta (Dept. Magdalena), an isolated massif near the north coast, are probably of very recent introduction since they are known as Papas Españolas (Spanish potatoes) to the primitive Indian tribes of that region.

(3) *Venezuela* : Most cultivation of subsp. *andigena* is to be found in Mérida State. In the lower regions near the north coast and in the low valleys of Mérida and Táchira states only subsp. *tuberosum* varieties are grown.

(4) *Ecuador, Peru and Bolivia* : The distribution of the tetrapoid potatoes of these three countries has been dealt with fully elsewhere (see Juzepczuk & Bukasov (1929), Bukasov (1930, 1933), Hawkes (1944)). There is some doubt as to the extent of potato cultivation in prov. Amazonas of Peru, and in the semi-deserts of S.W. Bolivia.

(5) *Chile* : Two samples of subsp. *andigena* were found by Montaldo (1951) in North Chile, Tarapacá province, behind Arica. It would be of some interest to know the extent of its cultivation in this province and also in Antofagasta and Atacama provinces at high altitude valleys (2500 m. and over), and it is to be hoped that some collector will make detailed collections and observations in these regions.

(6) *Argentina* : Subsp. *andigena* is certainly to be found in the northernmost province of Jujuy, as most collectors in those regions have shown, and which I myself have been able to verify. The collectors Petersen and Hjerting also mention its occurrence in Catamarca, Salta and Tucumán (personal communication), whilst Millán (1945) talks of potatoes being grown in the high valleys of San Juan and Mendoza, which may possibly belong to subsp. *andigena*. I myself have examined herbarium collections of this subspecies from Catamarca (*Diaz Peña* 125. Herb : LP) and Mendoza (*R. Leal* 5436, Mendoza, Dpto, Maipú, Luriaga. May 1937. Herb : LIL). I have no data for La Rioja but from the position and altitude of this province one may hazard a guess that subsp. *andigena* is to be found there also. Collecting expeditions in these regions would be of the greatest value in defining the southernmost range of subsp. *andigena* with more exactitude. If we find that it does indeed spread as far south as Mendoza (which the present data seem to show) it will be seen that there is a gap of only some 200 km., or possibly less, between it and the most northerly limit of subsp. *tuberosum*. On this evidence it does not seem so impossible that the Chilean subspecies was derived from the original Andean stock. The gap has been certainly bridged by a wild species, namely *S. maglia*, which I have identified from collections made in Mendoza as well as in the region of Santiago. We may therefore hope that further collections by Argentine botanists and potato breeders will supply the missing data to complete the distribution pattern of this interesting subspecies.

Weed or escaped forms of subsp. andigena.

Weed forms of this subspecies have been recorded as follows :

Mexico : (1) Puebla State, near San Martín, in cornfields, common. 14 July 1929. Alt. : 2500 m. *Ynés Mexía* 2658 (Herbs : BM, F, G-Del, MICH, NY, UC.).

Costa Rica : (2) Prov. Cartago, Volcán Irazú, Mt. Roble, Alt. : 2000 m. A weed in potato crops. *Hawkes* 1124 (seed and tuber collection only). Possibly a recent introduction ?

Colombia : Dept. Boyacá, L. Tota (3) Near Pueblo Viejo. 23 Sept. 1939. "Growing as a weed on the sides and furrows of potato cultivations, ditches, etc." 'Chava'. *Balls* 7455 (Herb : Potato Genetics Station, Cambridge) (4) Peninsula de Guayta. Alt : 3000 m. 4 Sept. 1948. 'Chava' or 'Paduana' *Hawkes* 333 (Herb : J.G.H.) (5) Isla Santa Isabel, 4 Sept. 1948. 'Paduana' or 'Clava' *Hawkes* 335 (Herbs : BOG, J.G.H.).

Ecuador: (6) " Aya papa ", mentioned by Bukasov (1933) as a subspecies of *S. andigena* should probably be grouped here. I have seen no specimen of it. (7) Prov. Cañar, Vitaliçia. 23 June 1939. " Not cultivated but grows spontaneously in the Indian plots and is used as food." ' Chihua ' or ' Chigua '. *Balls* 7107 (CPC : 649) (No herb. specimen). $2n=48$. (8) Prov. Cañar, Azogues, Quinta El Rosio. 25 June 1939. " Spontaneous in cultivations ". ' Zhio '. *Balls* 7117 (CPC : 635), (Herbs : J.G.H., Potato Genetics Station) $2n=48$. (9) Prov. Pichincha, near El Quinche, Iguiñaro. 18 July 1939. ' Sacha papa '. *Balls* 7241 (CPC : 825) (No herb. specimen) $2n=48$.

Peru: (10) Cuzco. July 1950. ' Sauki-aracka '. *Vargas* 811 (Hort : J.G.H. : CPC. 2404) (11) Ex Dr. H. Ross 50/89. From ' La Molina ': Peru, sent as ' *S. aracc-papa* ' (Hort. : J.G.H. : CPC. 2412).

Bolivia: (12) Dept. Chuquisaca, Sucre. Alt.: 8500 ft. 6 March 1939. " A weed of cultivation in maize fields and among stones at the edges of the field ". *Balls* 6146 (CPC : 161) (Herb : Potato Genetics Station, Cambridge). (13) Sucre, La Recoleta de San Francisco. Alt. : 8700 ft. 7 March 1939. ' Ppisco papa '. *Balls* 6171 (CPC : 174). (Herb : Potato Genetics Station, Cambridge.) Both these collections were described by me (1944) as *S. subandigena* Hawkes. (14) Dept. La Paz, prov. Larecaja, Valle de Tipuani. ' Lilicoya ' *Weddell* (1851) (Herb : P).

Most, if not all, of these potatoes may be escapes or natural segregates from higher yielding cultivated sorts. With their long creeping stolons and poor yield they have been able to survive as weeds in fields, walls and paths. They might possibly, however, be part of a pre-agricultural complex of tetraploid potatoes (if the tetraploid level was reached before the beginnings of agriculture) not brought into cultivation because of their poor yield and bad flavour, which survived as weeds in other crops. Further genetical work on these forms is needed to elucidate such problems (see also p. 139).

15. The Type of Subsp. *andigena*.

The type specimen for *S. andigena* on which the subspecies *andigena* is based was cited by Juzepczuk and Bukasov (1929) as *Juzepczuk* 598, from Central Peru, Department Junín, Cerro de Pasco. This specimen is presumably deposited in the Herbarium of the Institute of Plant Industry in Leningrad but I have not yet been able to see it or obtain photographic copies of it.

In his later, more detailed, study of *S. andigena* Bukasov (1933) makes no reference whatever to the type collection although he quotes numerous other collections from Central Peru. The only additional data that I have been able to find is in a cytological work by Rybin (1930) where the chromosome numbers of cultivated forms, collected by Juzepczuk and Bukasov are noted. Here we find number 598 I (does this " I " stand for Juzepczuk, or is it perhaps a misprint for " T ", indicating that the specimen in question was the type ?), which is stated as having been collected near Cerro de Pasco at a place called Titli-Caen. Unfortunately, this place name is not marked on any of the maps available to me, including the American Geographical Society's 1 : 1,000,000 edition.

Referring again to Bukasov's publication (1933) we read that " The Central Peruvian forms are taken as a typical variety and regarded as initial forms for the species ". When we come to review these same forms we find that they are grouped into the following taxa, namely : 1. var. *juninum* ; 2. f. *nodosum* ; 3. var. *platyantherum* ; 4. subsp. *tarmense* ; 5. f. *tenue* ; 6. var. *latius*, in the order given. None is described as collected in Cerro de Pasco, though var. *juninum* is said to be from Dept. Junín, in which Cerro de Pasco is situated, whilst f. *nodosum* is said to be from Titli-Caen, though not with the collection number 598.

We have no exact description or plate of the type specimen of *S. andigena*, and although we know that the typical forms are to be found in the Department of Junín, Central Peru, this does not necessarily mean that the type specimen was taken from amongst them. On the whole it seems probable that var. *juninum* is the one that Bukasov had in mind when he was describing the species, and it is in any case the first name on his list of Central Peruvian taxa. I shall therefore treat var. *juninum* (see fig. 8 and Pl. 5) as typical for the subspecies and cite the following collection as the one on which I base my interpretation of subsp. *andigena* :

Ochoa 36, collected in Peru, dept. Junín, Departamento de Pasco, Prov. Daniel Carrión, Alturas de Huariaca. Alt. 3600 m. 15 June 1947. Vernacular name ' Siruco ' (Herbs : J.G.H. C. Ochoa) (see Pl. 4).

This specimen fits reasonably well with the description given for var. *juninum.** The leaf (see Table 4) is a little less dissected (as will be seen by comparing fig. 8 with Pl. 4) but this is probably due partly to the fact that a greater degree of dissection seems to be developed on Russian grown than on S. American grown lines of subsp. *andigena.* I myself did not collect from Cerro de Pasco, so that this specimen of my friend Dr. C. Ochoa, of Huancayo, Central Peru, is particularly useful in these circumstances, particularly as it is of a plant actually grown in South America under conditions to which it is presumably well adapted.

16. ORIGIN OF *S. TUBEROSUM*.

The data that we have presented above all point to the fact that *S. tuberosum* originated in the Central Andes of Peru and Bolivia and spread north and south to Colombia and Chile, respectively. In Chile it differentiated into a separate geographical subspecies under the prevailing climatic and day length conditions of that region.

How did the tetraploid species *S. tuberosum* originate in the Andes and what were its probable ancestors ? To be able to answer this question we must consider the evidence obtained from cytological studies of this and related species. Bukasov (1939 a, b) considers that the tetraploid potatoes may have arisen either by the union of two diploid gametes from triploid species or by the fusion of unreduced gametes from diploid species. Since the nearest related triploid ' species ' are all hybrids between tetraploids and diploids, the former explanation is of little value in this case. Hawkes (1944) suggested that the tetraploids might have arisen by means of somatic chromosome doubling induced by heat, cold, wound damage, etc., or more probably from diploid species by the fusion of unreduced gametes.

If *S. tuberosum* arose from chromosome doubling or by fusion of unreduced gametes from the same species it would be an autotetraploid, and this should be discernible at meiosis. Alternatively, if it were an allotetraploid, derived either by the fusion of two unreduced gametes from different diploid species, or, more probably, by chromosome doubling in a natural hybrid between two species of low chromosome homology, this should also be discernible by cytological analysis. Studies of different varieties of this species by various workers (summarized by Swaminathan and Howard, 1953) show that there is a mean quadrivalent+trivalent frequency of between 2 and 3 per nucleus. This compares with a frequency of 4 in artificially produced tetraploid (i.e. autotetraploid) lines of *S. rybinii* and 0 in the allotetraploid species *S. acaule*. These data would seem to suggest, therefore, that *S. tuberosum* is not completely autotetraploid, but is perhaps an allotetraploid formed from two closely similar diploid species whose chromosomes were structurally similar. A study of

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* *Ochoa* No. 40 agrees even more closely with v. *juninum*. It does not, however, come from the type locality for *S. andigena*.

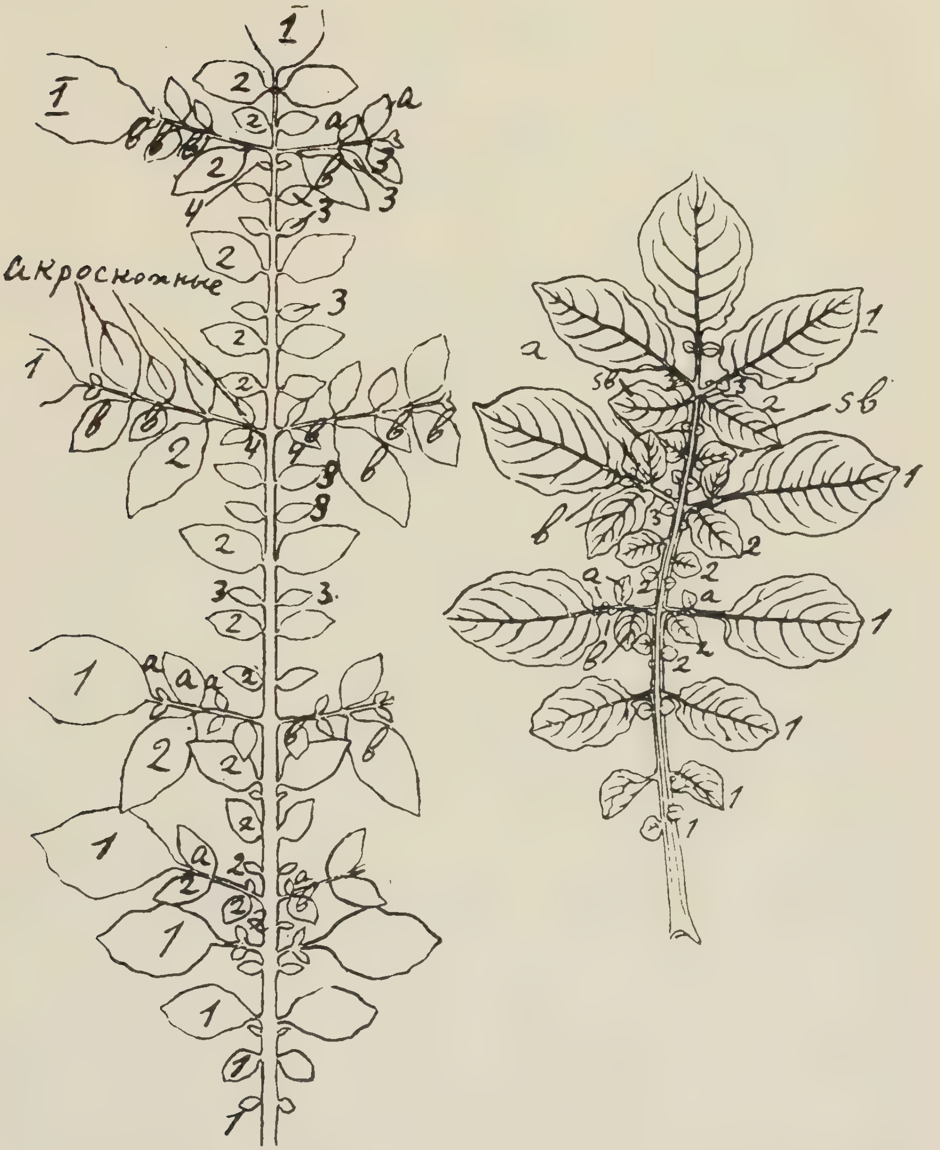

Рис. 1а. Схема рассеченности листа.
Слева—v. *juninum*, справа f. *caiceda*
1—доли 1 порядка основные.
2— „ 2 „ (дольки).
3— „ 3 „ (долечки).
4— „ 4 „
а—акроскопные дольки
в—базископные дольки
sв—полубазископные (угловые) дольки.

Fig. 1a. Scheme of dissection of the leaf.
On the left—v. *juninum*, on the right f. *caiceda*.
1 -- primary segments
2 — secondary „
3 — tertiary „
4 — quarternary „
a — acroscopic „
b — basiscopic „
sb — semibasiscopic segments

FIG. 8.—Leaves of subsp. *andigena*. Juzepczuk and Bukasov's type variety is on the left. (From Bukasov, 1933, fig. 1a.)

artificially produced haploids made by Ivanovskaya (1939) also suggested some differentiation of the two genomes of the gametic set of S. *tuberosum*. When artificial octoploids are made, they are found to be dwarf, thick-stemmed and slow-growing ; this, as pointed out by Lamm (1945), suggests that S. *tuberosum* is an autotetraploid.

Further evidence has been obtained recently by Gottschalk (1954), Gottschalk and Peters (1954) and Peters (1954) on the autopolyploid nature of S. *tuberosum*. These authors show that, in respect of the heterochromatic segments of its chromosomes the cultivated potato, both subsp. *tuberosum* and subsp. *andigena*, is a true autotetraploid and contains two practically identical genomes in its haploid chromosome set.

On the basis of these cytological data we can tentatively look for the origins of S. *tuberosum* in the mountain regions where the ancestral subspecies *andigena* is to be found in the greatest variety, namely in Peru and Bolivia. The following additional data point to the same conclusion :

(i) Very wide genetic variability ; presence of a large amount of diversity here that is not found in other regions.

(ii) Presence of several nearly related diploid cultivated species in the same area, some of which hybridize with it forming large numbers of triploids with reduced fertility. This situation is not found in N. Argentina, where there are no diploid cultivated species, or in Ecuador and Colombia, where although a diploid species is present (S. *phureja*) very few triploid hybrid clones are to be encountered.

(iii) Presence of nearly related wild and weed diploid species from latitude 10° S. (Central Peru) to 20° S. (Potosí, C. Bolivia), growing in the same areas and forming one ecological group with it. (Diploid wild species are also found in N.W. Argentina to about 28° S.).

(iv) The evidence of very ancient civilizations in this area is also suggestive of the ancient culture and perhaps origin of the tetraploid potato in this region.

Hence we must look for the original diploid ancestor of S. *tuberosum*, either amongst the primitive diploid cultivated species of Bolivia and Peru, namely, S. *stenotomum** Juz. et Buk., S. *goniocalyx* Juz. et Buk., S. *ajanhuiri* Juz. et Buk. and S. *phureja* Juz. et Buk. or amongst the diploid wild or weed species of the same area.

It will first be necessary, however, to discuss the problem of whether S. *tuberosum* arose from wild or cultivated ancestors. The evidence on the whole seems to be rather in favour of the latter alternative—that it was derived from a cultivated form and not from a wild one. The arguments for this are as follows :

(1) The type of genetic variability in the primitive diploid cultivated species and in S. *tuberosum* is very similar. There is some evidence for the presence of actually similar or identical genes in these diploid and tetraploid cultivated potatoes, a fact that fits well with the explanation that the latter were directly derived from the former. If we assumed that they originated independently from distinct wild ancestors the presence of similar genes would be harder to explain. We must bear in mind, however, that there is very probably a certain amount of gene flow from the diploids to the tetraploids and vice versa by means of the partially sterile triploid species S. *chaucha*†. This can be back-crossed artificially to both parent species forming a small percentage of moderately fertile back-cross hybrids. Hence introgression and exchange of genes between the diploid and tetraploid potatoes is very possible.

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* Eleven diploid species have been described up to now but experimental studies indicate that only the four mentioned above should be considered valid. A full account of the taxonomy of this group is in course of preparation.

† Formed as a hybrid between S. *stenotomum* (2×) and S. *tuberosum* subsp. *andigena* (4×).

(2) If we examine the distribution data of the 'wild' or 'escaped' forms of S. *tuberosum* (see pp. 129 and 134) we find that they occur sporadically in widely separated localities. This fact accords better with the view that these forms are casual escapes or "reversions" from a widespread cultivated species, rather than that they are relics of a formerly ubiquitous wild tetraploid most of which has been taken into cultivation. These 'escaped' forms are in fact known from as far north as Mexico, Costa Rica and Colombia, and as far south as southern Chile, having therefore a wider (though more disjunct) distribution area than any known species of truly wild potato. It is far easier to conceive that this wide distribution is in fact due to the original tetraploid cultigen having been carried by man over this very wide area.

(3) No truly wild tetraploid that is closely related morphologically, cytologically or genetically to S. *tuberosum* has yet been found. Many travellers and collectors have searched in vain for the original wild potato. All the so-called wild ancestors such as the triploid species S. *maglia* Schlecht. and S. *commersonii* Dun., and the tetraploid S. *longipedicellatum* Bitt. have later been shown to belong to quite distinct taxonomic groups. I was at one time inclined to think that this absence of S. *tuberosum* as a wild plant might be explained by assuming that it had been taken into cultivation almost in its entirety. It seems more probable, however, that it never existed in the wild but originated from an already existing diploid cultigen.

(4) The Chilean 'wild' forms of S. *tuberosum* possess a gene for red tuber colour which is not found in any other wild species but which does occur both in the diploid and the tetraploid cultivated complexes. This again indicates that the Chilean forms at any rate are escapes from cultivation and are not primitively wild.

If we accept as a working hypothesis, then, the view that S. *tuberosum* originated from a previously cultivated diploid species we can examine the diploid material to see whether any of the species occurring at the presumed centre of origin of S. *tuberosum* may have contributed to its formation.

Of the four diploid cultivated species mentioned above (see p. 138) one, S. *ajanhuiri*, is very restricted in geographical range and is of limited variability. Certain features lead one to suspect that it was derived fairly recently by complex natural crosses from S. *acaule* (a wild tetraploid species) and S. *stenotomum via* the triploid hybridogenic species S. *juzepczukii*. It is therefore very doubtful whether S. *ajanhuiri* could have had anything to do with the origin of S. *tuberosum*.

When we turn to the species S. *goniocalyx* in Central Peru we find that its distribution does not coincide with the region of greatest diversity of S. *tuberosum*. Furthermore, the range of morphological and genetical variability in S. *goniocalyx* is small, leading one to suppose rather that it might be a northern derivative of the widespread species S. *stenotomum*. This latter view has also been put forward by Emme (1937).

The third diploid species to be considered, namely S. *phureja* (including S. *rybinii*), is found widely distributed from Venezuela and Colombia southwards to Central Bolivia. It is, however, very distinct from S. *tuberosum* in its ecological requirements, since it is confined to the wetter lower altitude zones of the eastern flanks of the Andes in Bolivia and Peru (Yungas, Ceja de montaña) and the high-rainfall mountain forests of Ecuador and Colombia. It is characterized by early maturity (3 months*) and complete lack of tuber dormancy. Neither of these two features are to be seen in S. *tuberosum*, nor is it grown in the same phytogeographical regions. S. *phureja* also, therefore, can be dismissed with a fair amount of certainty as the possible diploid ancestor of the tetraploid potato.

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* Maturity time refers to South American conditions only.

Finally, we must consider *S. stenotomum*. This species is widely distributed in S. Peru and N. Bolivia and is also cultivated in great quantity, especially among the Indians. The genetic variability is immense, quite comparable with, if not exceeding, that of *S. tuberosum* itself. Furthermore, *S. stenotomum* is grown in the same regions (often in the same fields) as *S. tuberosum* and is adapted to the same ecological conditions. It differs from *S. tuberosum* in the more delicate habit, narrower leaflets, and in the lengthened calyx lobes which are generally disposed irregularly in groups of two or three (bilabiate). However, certain Bolivian forms possess a much smaller, more regular calyx, not too far removed in shape from that of *S. tuberosum*.

The morphological, genetical and ecological data, therefore, point fairly clearly to *S. stenotomum* as the ancestor of *S. tuberosum*, and this is confirmed by the cytological findings of Gottschalk and Peters* (1955). Pachytene analyses made by these authors showed a close structural similarity in ten of the eleven identified chromosomes of *S. stenotomum* with those of *S. tuberosum*. No such close structural similarity could be shown for *S. goniocalyx*, *S. phureja* (as *S. rybinii*) or *S. ajanhuiri*, all of which exhibited considerable differences in their pachytene chromosomes when compared with *S. tuberosum*. Certain wild species such as *S. simplicifolium* and *S. vernei* were even more widely removed, though these workers have not yet been in a position to analyse the diploid wild and weed species that also show the greatest morphological similarities to *S. tuberosum*.

As we have already mentioned, a number of cytologists have considered that *S. tuberosum* might be an amphidiploid hybrid between two species whose genomes were basically similar, though differentiated to some extent. This conclusion is considered to be inadmissible by Gottschalk for the reasons given in the preceeding paragraph. We shall, however, review the evidence put forward, since, in view of the lack of complete genome differentiation in the tuber bearing South American potatoes a very wide range of diploid species could cross together giving moderately fertile hybrids.

Genetical evidence, in addition to that provided by Gottschalk, shows that crosses, between *S. stenotomum* and *S. phureja* could have played no part in the formation of *S. tuberosum*. Thus, in crosses between these two species Emme (1937) showed that the calyx shape of *S. stenotomum* was dominant, and hence very dissimilar from that of *S. tuberosum*. Similar results have been obtained by the present author who also found that the short dormancy of *S. phureja* was fairly well marked in the F_1 generation. Since this distinctive bilabiate calyx of *S. stenotomum* is not found in *S. tuberosum* and since the growth and dormancy characteristics of *S. phureja* are also absent from the tetraploid species we may conclude from these data also that *S. phureja* played no part in the formation of *S. tuberosum*.

A possible second ancestor of *S. tuberosum*, however, might be the diploid weed species *S. sparsipilum* (Bitt.) Juz. et Buk. This species in its wider sense includes as synonyms various diploid weed species from Bolivia and Peru such as *S. lapazense* Hawkes, *S. araccpapa* Juz., *S. bukasovii* Juz. and *S. calcense* Hawkes. It is found abundantly in and around potato fields at high altitudes and in the same ecological regions as *S. tuberosum* and *S. stenotomum*.

Its wide range of variability induced both Juzepczuk and myself to consider it previously as several distinct species. When I began experimental studies with these 'species' I found that both F_1 and F_2 generations of hybrids between them in various combinations were quite thrifty and fertile. It seems therefore more reasonable to look on them as belonging to a widespread polymorphic weed species. The calyx and corolla of *S. sparsipilum* are very close indeed (though somewhat smaller in all dimensions) to those of *S. tuberosum.* The leaves are closer to the less dissected leaf of certain varieties, especially the Bolivian forms, of *S. tuberosum,* whilst the tubers are of the usual unpigmented wild type.

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* These authors postulate the derivation of *S. tuberosum* from an ancestor of *S. stenotomum*, not from this species itself as known to us at the present day.

In artificial hybrids between *S. stenotomum* and *S. sparsipilum* (Family 135) the calyx shape of *S. stenotomum* is recessive to that of *S. sparsipilum,* so that the F_1 hybrids are very close indeed to *S. tuberosum.* An amphidiploid from these has not yet been obtained but might probably show an even greater degree of resemblance.

Both *S. stenotomum* and *S. sparsipilum* possess a large amount of variability, so that if *S. tuberosum* was produced on several occasions as a result of natural crosses with subsequent chromosome doubling a large amount of the genetic variability of both parents might have been transferred to their tetraploid derivative. Alternatively if there was only one initial cross the variability within *S. tuberosum* might have been increased gradually by gene flow via the triploid hybrids—a fact to which we have already referred.

Unfortunately, pachytene analyses of *S. sparsipilum* have not yet been completed, so that, although from morphological genetical and ecological evidence we can say that *S. sparsipilum* stands very close to *S. tuberosum* and may perhaps have played some part in its formation, cytological evidence is not as yet available. If the genome of *S. sparsipilum* does show great structural agreement with those of *S. stenotomum* and *S. tuberosum* we shall perhaps need to reconsider the taxonomic position of the two diploid species in the light of this evidence.

We can tentatively consider, then, that *S. tuberosum* arose either directly from an ancestral form of *S. stenotomum* by a process of simple chromosome doubling, or as a spontaneous amphidiploid hybrid between the more ancient diploid cultigen *S. stenotomum* and the diploid weed species *S. sparsipilum.* The evidence at hand seems more strongly in favour of the former hypothesis.

We shall consider the evidence for the origin of *S. stenotomum* elsewhere but it may be remarked at this stage that there are a number of imperfectly studied wild species in S. Peru and N. Bolivia which are probably related to it. Cytological analyses are being made of these closely related diploid weed and wild species ; and it is hoped that more conclusive evidence may soon be forthcoming. It seems highly probable, however, from the evidence we have been reviewing, that *S. stenotomum* or its immediate ancestor has played the most important role in the formation of the tetraploid cultigen *S. tuberosum.*

Thus by the close integration of experimental studies on the one hand and formal taxonomic analyses on the other, we are obtaining an insight not only into the relationships and mode of evolution of the cultivated potato *Solanum tuberosum,* but also into that of the other tuber-bearing species in this genus.

17. Summary.

The origin and interrelationships of the tetraploid potatoes grouped under *Solanum tuberosum* L. are discussed. In the designation of a nomenclatural type for *S. tuberosum* the early descriptions of C. Bauhin, Clusius, and others are mentioned in relation to those of Linnaeus. Evidence is brought forward to show that one of the three specimens in the Linnean Herbarium labelled as *S. tuberosum* may be considered as the lectotype. It is then pointed out that Linnaeus' description, made only when one species of tuberiferous *Solanum* was known, could equally well be taken as referring to some 80 per cent of the subsequently described wild species. A new description has therefore been drawn up which attempts to include the complete range of variability of *S. tuberosum* under modern concepts, and this is followed by reference to the main features that distinguish it from other potato species.

The views of the Russian taxonomists on the subdivision of the cultivated tetraploid potato into two distinct species are next outlined. The criticisms levelled at these views show that it is impossible to separate the cultivated tetraploids into more than one species and that the weed tetraploids previously described as distinct should also be included within *S. tuberosum*. These views are also reinforced by experimental data.

An analysis of the difference between the Andean and Chilean South American potatoes makes it possible to recognize two subspecies, namely (*a*) subspecies *andigena* from the mountains of Venezuela, Colombia, Ecuador, Peru, Bolivia and N. Argentina, (*b*) subspecies *tuberosum* from Europe and South Chile. That the European and Chilean potatoes are included under the same subspecific name does not imply that the former were derived from the latter; but that each evolved under similar environmental conditions from original Andean stocks.

In discussing the problem of the origin of the tetraploid potato it is shown that it can be considered as an autotetraploid, but may have been formed as an amphidiploid hybrid between two species whose genomes were not quite identical.

The evidence at hand points to the conclusion that *S. tuberosum* was derived from an already cultivated diploid species and not directly from a wild one. It seems probable, for a variety of reasons, that the cultivated potato *S. stenotomum* or a precursor of this species was the original diploid ancestor of our tetraploid potato. Evidence is also put forward to show that the weed diploid *S. sparsipilum* may also have played some part in the formation of *S. tuberosum*, though cytological opinion is more strongly in favour of *S. stenotomum*.

18. Addendum

Since this paper went to press Dr. S. M. Bukasov has very kindly sent me a photogaph of the type specimen of *S. andigena* Juz. et Buk. This was made from plants grown near Leningrad in 1929 from tubers collected by Juzepczuk (No. 598) in the vicinity of Cerro de Pasco, dept. Junín, Peru. The name " Titli-Caen " is not mentioned on the herbarium label, nor is any varietal rank (e.g. var. juninum) given to the specimen.

Unfortunately the photograph came into my possession too late for its inclusion in the present paper, but it is worthy of note that the leaf differs very little from Ochoa's collection No. 36 (see plate 4) on which I have based my own interpretation of *S. tuberosum*, subsp. *andigena* (see p. 136). The leaf indices of the specimens in question are as follows :—

Juzepczuk	No. 598	Index 59
Ochoa	No. 36	,, 55

The difference in the index value between the two specimens is very small and could easily be accounted for by the fact that the former specimen was taken in Russia and the latter in Peru.

It is of further interest to note here that the leaf dissection in the type specimen of *S. andigena* is not so extreme as that figured by Bukasov for var. *juninum* but is roughly intermediate between that and his diagram on the leaf of f. *caiceda* (see Fig. 8, p. 137).

In conclusion, then, we can state that Juzepczuk's specimen No. 598, which was used by him as the type for *S. andigena* Juz. et Buk., must also be taken as the type for *S. tuberosum*, subsp. *andigena* (Juz. et Buk.) Hawkes. Ochoa's collection No. 36 is sufficiently similar to that of Juzepczuk for it to be considered as a useful basis for subsp. *andigena* when the type specimen is not available for study.

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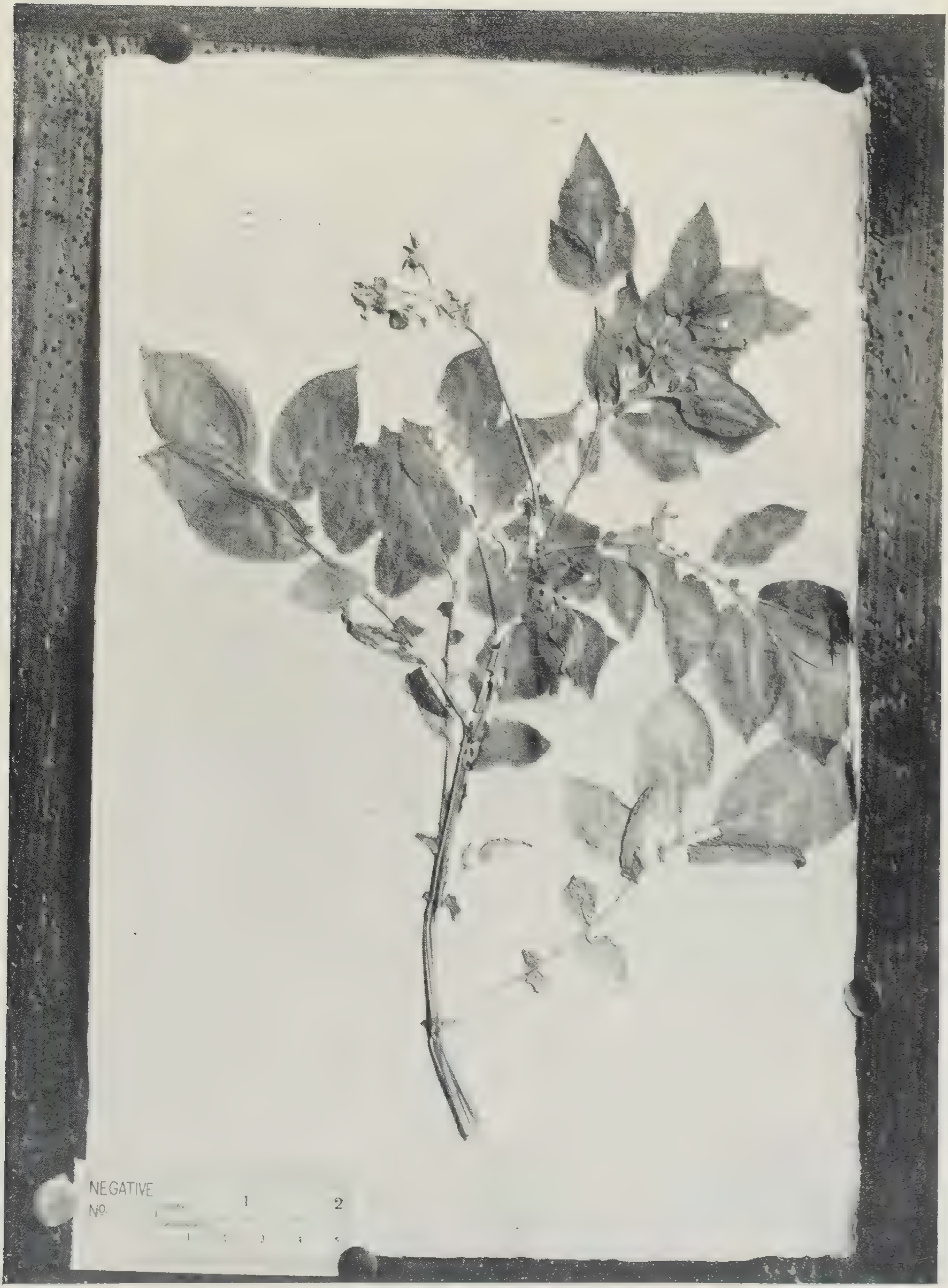
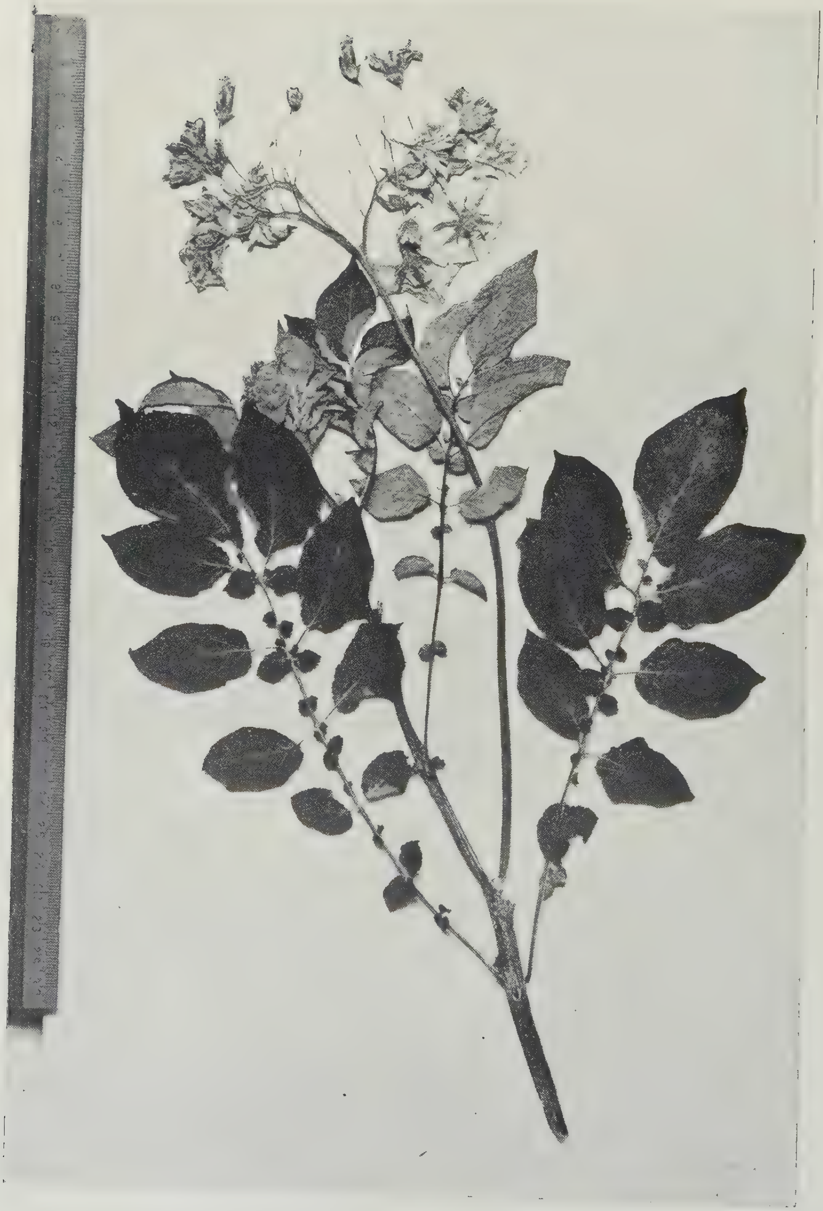
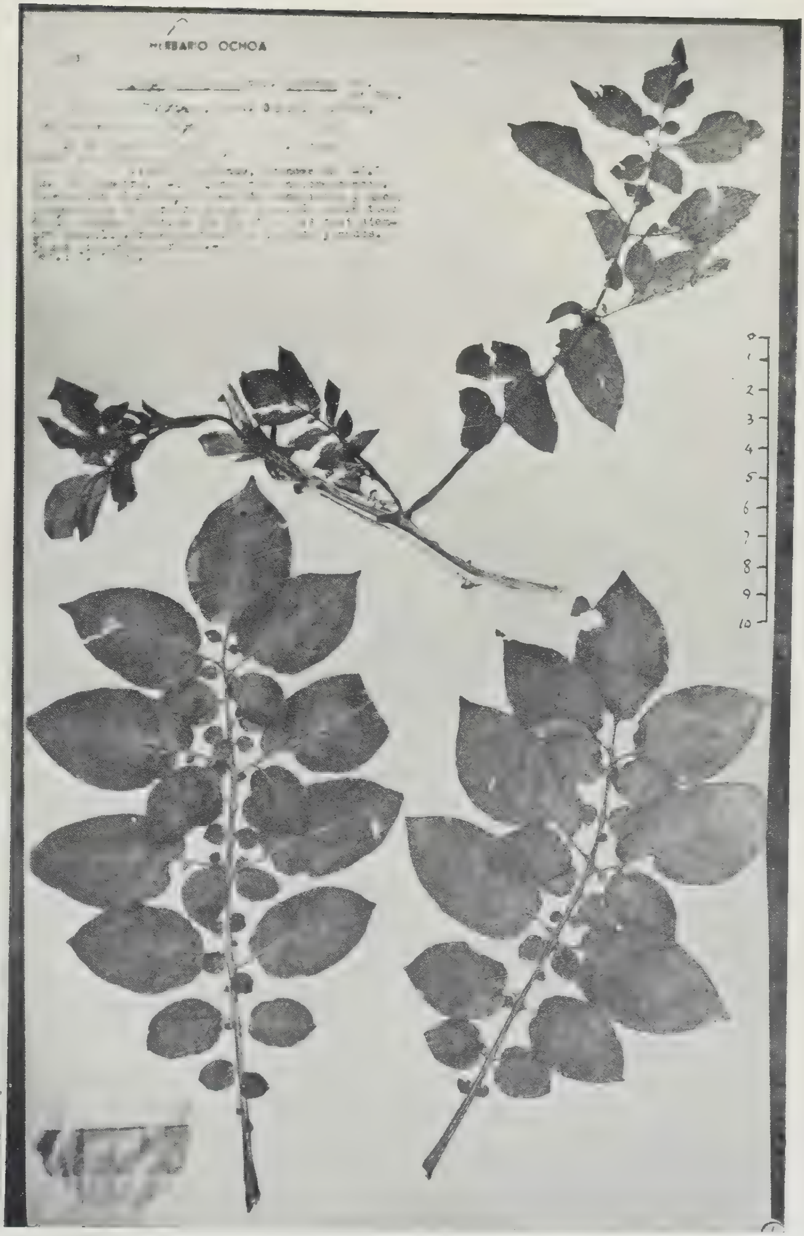


Solanum tuberosum L. Lectotype in Herb. Linn., No. 248·12.



Solanum tuberosum L., subsp. *andigena* (Juz. et Buk.) Hawkes. Casper Bauhin's herbarium specimen of the cultivated potato in Herb. Basel.



Solanum tuberosum L., subsp. *andigena* (Juz. et Buk.) Hawkes. A typical collection of the subspecies on which the interpretation of the present author is based ; collected in Peru, dept. Junín, Huariaca. *C. Ochoa* 36 (Herb. J. G. H.). Leaf index : 52.

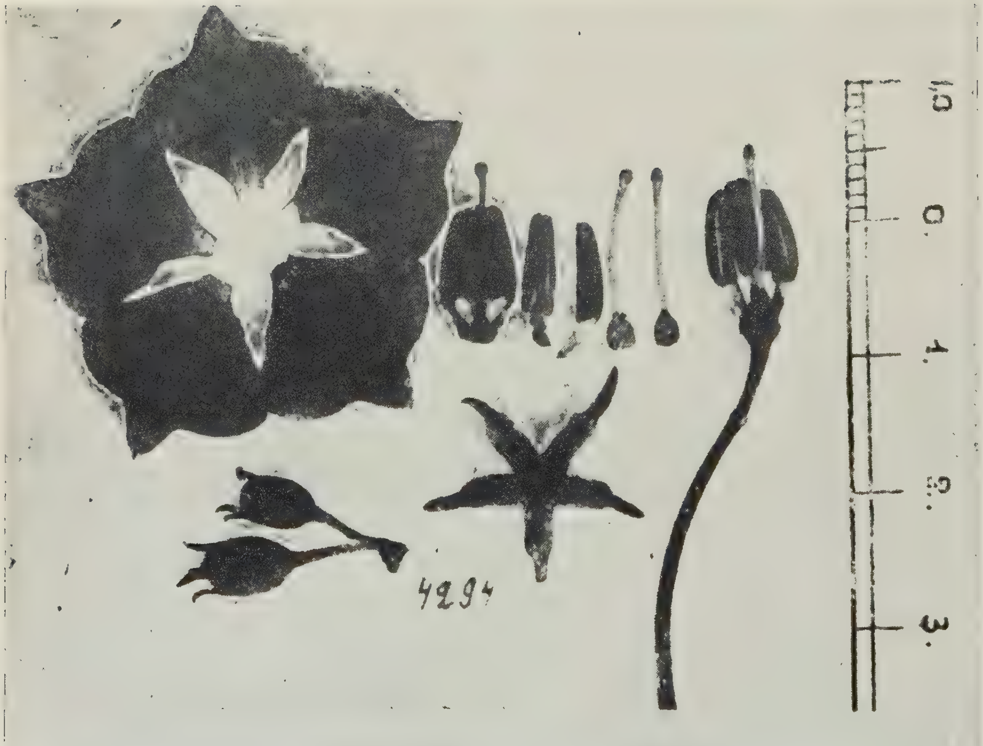


Рис. 10. Детали цветка var. *juninum* (шкала в см.).
Fig. 10. Details of the flower of *S. andigenum* var. *juninum*.

Details of the flower of Juzepczuk and Bukasov's var. *juninum* from Central Peru (from Bukasov, 1933, fig. 10).

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THE PRESENT AND PAST VEGETATION OF SPITSBERGEN

By Ove Arbo Høeg.

Abstract,—

In Norway the word Svalbard is now often used as a synonym for Spitsbergen. The two words, however, do not have exactly the same meaning. Svalbard is the name for the whole area which, in 1925, was placed under Norwegian administration. It lies between lat. 74° and 81° N. and between long. 10° and 35° E. Gr., comprising West Spitsbergen, North-East Land, Bear Island, and other islands, with a total land area of about 24,000 sq. miles (62,050 km.^{2}), that is, something between Denmark (44,000 km.^{2}) and Scotland (79,000 km.^{2}).

West Spitsbergen is Spitsbergen proper. Apart from some meteorologists on Bear Island it is the only island with a permanent habitation. It is this island that is called Spitsbergen in the following pages.

Although the climate of Spitsbergen is exceptionally favourable if compared to that of other countries of the same latitude, the present flora there is living under very severe conditions.

The mean annual temperature varies from year to year between *c.* −3° and −6° C. Only in the four months from June to September is the mean temperature above the freezing point, and in the warmest month, July, it varies from *c.* 3·5 to 5°.

The secular change in the temperature which has taken place in north-west Europe has been more pronounced in Spitsbergen than further south (Hesselberg & Birkeland, 1940). The increase in mean annual temperature in about 50 years has been calculated to be 2–3° C. This is chiefly due to an increase in the winter temperature, which has gone up by *c.* 5°, while the increase in the warmest month, July, is insignificant. Since the summer temperature is by far the most important climatic factor for the plants in Spitsbergen, the change that has taken place has scarcely had such a great effect on the vegetation as one might expect judging from the rise in the mean annual temperature.

The question of the regression of the glaciers in Spitsbergen is interesting and complicated. As in Norway, but perhaps in a still higher degree, it is easy to see that they have regressed. There are terminal moraines at shorter or longer distances from the ice front, and the lower parts of the glaciers are surrounded by naked rocks which have not yet been taken in possession by lichens or other plants. Nobody, however, knows when the regression started or when it reached (or will reach) its maximum. In recent years the glaciers are evidently not regressing ; on the contrary, there are some which have been growing. There is not necessarily any contradiction between this fact and the rise in the mean temperature. The rise in temperature is probably caused by southerly winds which are not only warm, but also moist. Therefore, although there are no reliable data on the precipitation in Spitsbergen over a period of sufficient length, it is quite probable that there has been an increase in precipitation in the form of snow on the glaciers, and this increase may have more than counter-balanced the increased melting.

The annual precipitation is about 250 to 300 mm. In a hot climate this would mean arid conditions, while in Spitsbergen it is sufficient, at least for a vegetation of the character prevailing there.

The *vascular plants* in Spitsbergen comprise 143 species. The tallest plants are shrubs of *Betula nana* which grow in a few sheltered places, and *Empetrum hermaphroditum.* Also *Cassiope tetragona* is a shrub which may grow to the height of a well-grown heather.

In marshy places, and in a few other types of plant communities, grasses, *Eriophorum,* and other monocotyledons may be dominant but on the whole the dicotyledons are the most numerous plants, in species as well as in individuals. By far most of them have flowers originally adapted to insect pollination, and the size of their flowers and the brightness of their colours are striking.

The general impression of the vegetation on a fine summer day is such that one would expect a fairly rich insect life. However, even on a calm and warm day the insects are scanty and comprise almost exclusively small diptera. Humble-bees do not occur at all (as they do for instance in Novaya Semlya); the absence of such plants as Papilionaceae, Labiatae, and *Aconitum* is probably connected with this fact. The great majority of the bright-coloured flowers in Spitsbergen are radial, simple, and evidently adapted to such simple pollinators as small flies. But even so they do not rely on the insects.

An investigation of the flower biology on islands at the north-west corner of Spitsbergen, and in the Ice Fjord and Wijde Bay areas (Høeg, 1932), showed that only one species, *Silene acaulis,* is regularly pollinated by insects. In *Silene* there are male and female individuals, the female ones usually bearing capsules, which must be the result of insect pollination ; however, the species has also hermaphroditic individuals which are able to pollinate themselves if insect pollination fails.

Some other species are also visited by insects so frequently on good summer days that cross-pollination takes place. This is especially the case with *Ranunculus*, *Dryas*, some species of *Saxifraga*, and a few more. But even these plants are able to pollinate themselves, thanks to the movements of the stamens, which bring the anthers in touch with the stigma. All other, originally entomophilous plants have either the same form of spontaneous autogamy as a regular feature, or they open their anthers in the flower buds (like *Pedicularis*), or they have given up seed formation altogether and resort to vegetative propagation. (As regards *Cassiope tetragona*, see Høeg 1932.)

The phytogeographical relationship of the Spitsbergen flora offers many problems which are far from being cleared up.

A number of the species (of vascular plants as well as thallophytes), which are common in Spitsbergen, are also widespread in Norway.

Another group of species, which forms an important part of the flora, belongs to an arctic–amphiatlantic element. They are found in Spitsbergen, North Greenland, Novaya Semlya, and some of them farther out beyond that area. If they occur in Scandinavia at all they belong to our rarest species and generally have a peculiar distribution. It is impossible to understand the mode of occurrence of this flora element in Spitsbergen without assuming that it has a high age. There is a strong indication that it has survived at least the last Ice Age in Spitsbergen, most likely in North Spitsbergen (see Lynge, 1933, 1941 ; Dahl, 1946).

There is a striking contrast between, on one side, the present vegetation and the severe conditions to which it is adapted, and on the other side the vegetation of the geological past, which bears witness of different ecological conditions.

The *geological structure* of Spitsbergen (Orvin, 1940, 1947) is extremely varied, comprising sedimentary rocks from practically all periods. Fossil plants have been found in a number of formations (cp. Nathorst, 1910) :

(1) *Downtonian and Devonian.* This formation has been estimated to have a thickness of approximately 9000 metres, mostly consisting of red or grey sandstones and some shales. Its upper limit corresponds to the top of the Middle Devonian.

The flora of the Downtonian (Høeg, 1942) is poor, but interesting. It comprises, undoubtedly, vascular plants, like *Zosterophyllum*, together with *Prototaxites* and *Pachytheca.*

The Devonian comprises a number of beds with plants preserved as impressions and, in the Middle Devonian, a few remains in the form of petrifications. Some of the genera, and probably also species, are identical with those which have been found in other parts of the world, while others so far have to be regarded as endemic. The most important ones are :

Drepanophycus sp.	Genus widespread
Psilophyton arcticum O.A.H.	Genus widespread, species endemic
Psilodendrion spinulosum O.A.H.	Endemic
Svalbardia polymorpha O.A.H.	Endemic
Hyenia (*Hyeniopsis*) *Vogtii* O.A.H.	Genus found elsewhere in Europe. Subgenus and species endemic
Enigmophyton superbum O.A.H.	Endemic
Actinopodium Nathorstii O.A.H.	Endemic

None of these plants, whether endemic or not, bears the slightest trace of having grown under conditions which we now would call arctic.

There is a coal seam in the Middle Devonian (Vogt, 1941).

The Upper Devonian is not represented in Spitsbergen proper, but in Bear Island, with coal seams and a well-developed *Archaeopteris* flora, in which the fern-like leaves have reached a width of at least 1 metre and probably more.

Culm. Slight subsidence with intensive sedimentation of sandstone (rather pure quartz), conglomerate, shale, deposited in fresh water or in brackish water, and coal. Many fossil plants, related to the contemporaneous flora of Central Europe. The lithological character of the sediments as well as the flora indicate that the climate was warm.

Upper Carboniferous and Permian. Marine limestone, then hiatus.

Triassic. The earliest Triassic (formerly thought to be Permian) is mostly marine, followed by continental sandstones and shales with plants, also some thin seams of coal.

Jurassic. A monotonous sequence of shales (Aucella shale), marine, lasting well into the Cretaceous period.

Cretaceous. Above the Aucella shale follows a continental series with plants, formerly called Jurassic, but now regarded as lowermost Cretaceous (*Ginkgo, Podozamites, Elatides*, etc.). On the whole the development of the Jurasso-Cretaceous is boreal, resembling the development in the Russian arctic area. The flora, however, is entirely of an ubiquitous type. There is fossil wood with growth rings (such rings are not found with certainty in the older woods known from Spitsbergen). They bear witness of a certain seasonal variation in the climate, but not the slightest indication of arctic conditions. There are also coal seams.

Tertiary. Up to 2000 metres of sandstone, shale and conglomerate, predominantly deposited in fresh water, but with a few marine beds. In the lower portions there are coal seams. The whole sequence has been regarded as not younger than Eocene ; however, the age question has scarcely been settled with full reliability.

The fossil flora of the Tertiary is rich in species and spread over a number of horizons. There is an abundance of silicified wood of conifers with growth rings, remains of *Equisetum* in situ, and twigs of conifers, preserved as impressions with cuticles. There are also fern leaves. By far the greatest part of the plant fossils, however, are impressions of leaves of dicotyledonous deciduous trees. This flora needs a revision, but its general phytogeographical character is clear enough. In the modern flora it has its equivalent in the temperate zone.

A palynological study of the Tertiary coals, carried out during the last three years by Svein Manum (1954), has shown that there is an abundance of pollen and spores, varying in quantity from seam to seam. In spite of the unsatisfactory preservation it has been possible to establish as least 52 different sporomorphs, which extend our knowledge of the Spitsbergen Tertiary flora quite considerably.

In the Arctic zone no other country combines the proximity to the pole with such a rich and varied fossil flora as Spitsbergen. This fossil flora presents innumerable problems of ecological, physiological and phytogeographical nature, problems which are accentuated by the contrast between the present flora and the floras of the past.

The present flora of Spitsbergen consists of plants whose morphology in many ways shows that they are adapted to the extreme conditions under which they live. They are dwarf, with short internodes, small leaves, and if they have lignose stems the annual growth rings are so narrow that they generally consist of only a few cell layers. Not a single fossil plant, from any geological formation, shows any of these morphological characters. The production of organic matter by the present-day vegetation is very slight and although the decomposition of organic remains takes place at a slow rate practically no peat is formed. In previous geological periods coal, as just mentioned, has been formed repeatedly, from the Middle Devonian onwards, testifying that the conditions, although not necessarily tropical, were fairly warm and humid.

How was it possible that such a vegetation could live at a distance of only 10° to 12° from the North Pole ? We do not know. It is, however, interesting to consider some of the factors which must have been different from those of the present days.

Among such factors, the temperature is no doubt the most important one. The Tertiary flora of Spitsbergen was composed of genera whose living relatives to-day are chiefly found in the U.S.A. and in China, partly also in Europe. There are no Malayan elements, like those abundantly represented in the Eocene London Clay. There are no palms or other plants suggesting a tropical flora or even a warm temperate one. If one can judge by the requirements of the living relatives, the summer temperature must have been at least as high as it is in Central Europe to-day. If that has been the case, and the summer was sufficiently long, the winter temperature would probably not matter very much. Certainly there is a varying degree of resistance to low winter temperatures among the trees, but it is surprising how many of them are able to resist a cold winter if their shoots have ripened properly.

Is it conceivable that the summer in Spitsbergen has been warm enough, and how could such a difference from the present conditions be explained ?

Some scientists, and among them palaeobotanists, have regarded the displacement of continents as the solution to most problems of palaeogeography. It is true that the fossil plants offer some problems to which continental drift *seems* to be the only solution (particularly the *Glossopteris* floras together with Permocarboniferous glaciations), but on the other hand, so many problems are left unsolved by the drift hypothesis, and so many new problems raised, that in my opinion one should try to find other solutions.

There is the possibility of a shifting position of the earth's axis. However, in addition to the serious objections raised by the geophysicists there is strong palaeobotanical evidence against the idea. Thus, there are Tertiary floras (certainly not exactly contemporaneous) all round the Arctic basin. Any attempt to shift the North Pole in order to get one of these floras to a lower latitude, would bring the Pole closer to one of the other localities.

Probably it is unnecessary to resort to hypotheses like these. Throughout geological history a warm climate in the Arctic is the rule. The exception is rather the Quaternary Ice Age, in whose shadow we still live, and it is the Ice Age that has to be explained, rather than the warmer climate. An increase in solar radiation leads to increase in atmospheric movements. What would be the effect of more intensive atmospheric movements, and what would happen if the enormous ice masses of the Arctic Sea, of Greenland and the Antarctic Continent were not there ? They consume so much of heat that the summer temperature is prevented from rising so much as it might otherwise have done.

Replies to these and similar questions would probably go a long way to solve our problem of Arctic fossil floras. The replies, however, have to be given by the meteorologists.

There are also other interesting problems connected with the ecology of Arctic forests, with the complicated interrelationship between the various plants, insects, soil microflora, and so on. To mention only one point : The photoperiodic effect of the continuous summer day. It would be interesting to know how the various tree species, which are modern relatives of the extinct ones of the Spitsbergen Tertiary, react to different day lengths and to what extent they are adaptable (cp. Høeg, 1937).

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PRESIDENTIAL ADDRESS

The Continental Drift Theory and the Distribution of the Copepoda.

By R. B. Seymour Sewell.

It has been said that scientists in their search for truth are nowadays too much concerned with the accumulation of facts, and make too little use of their imagination in their attempts to explain such facts as they have accumulated. So in selecting a subject for my Address to you this evening I decided to try to see to what extent the facts that have been accumulated regarding the occurrence in different regions of the world of some of the Copepods can best be explained by one or other of the two main theories that have been put forward regarding the manner in which the present distribution of land and sea was achieved. These two theories are those of " The Permanence of the Ocean Basins " and " The Continental Drift ".

The older theory, that of the permanence of the ocean basins, is still widely accepted by many geologists and geophysicists, and rests on the assumption that the great oceans have always occupied the positions in which they are found to-day, though this assumption has had to be modified to the extent that it is supposed that in times past many of the continents were in one epoch or another directly connected by means of wide or narrow land ' bridges ' that have since disappeared. One of the most important of these ' bridges ' is supposed in Palaeozoic and early Mesozoic times to have connected the Brazilian part of South America with the greater part of Africa in the Southern Hemisphere, while another connected North America and Europe in the Northern Hemisphere : other ' bridges ' are supposed to have connected Africa with India, India with Australia and Australia with Antarctica. Thus the land masses of the Southern Hemisphere according to this theory must in Permo-Triassic times have presented an appearance as of a great horse-shoe enclosing a large southern Mediterranean Sea, which presumably was connected with what is now the south-eastern part of the Pacific Ocean through Drake's Strait (fig. 1) ; or, alternatively, South America was connected across Drake's Strait with Antarctica and the Mediterranean Sea opened into the south-western part of the Pacific through a gap between Australia and Indo–Malaya. According to this theory the South Atlantic and Indian Oceans were at this period only vaguely foreshadowed by two wide bays in the northern shore-line of this enclosed sea.

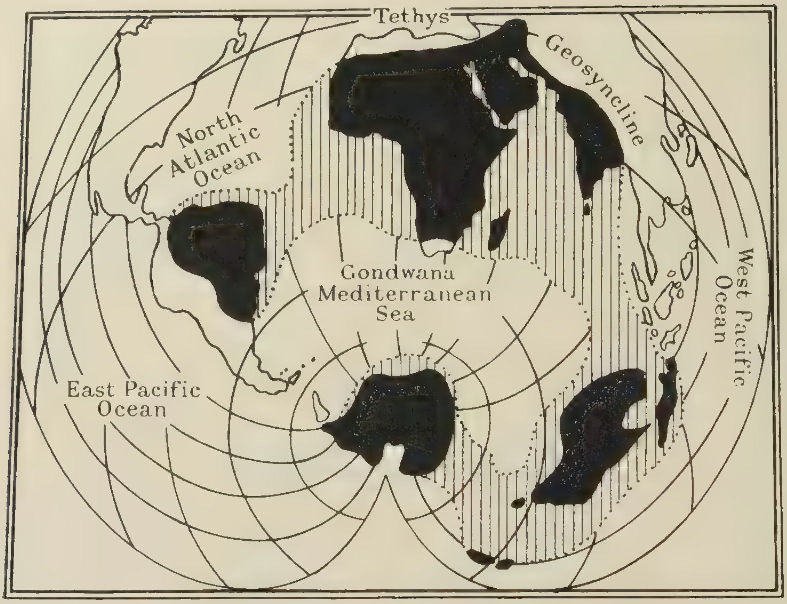

FIG. 1.—Gondwanaland in the Permo-Triassic Epoch, according to the theory of the Permanence of the Ocean Basins.

The second theory, frequently referred to as " The Wegener Drift Theory ", though more properly termed " The Theory of Continental Drift ", has received support from many biologists and from some geologists : since its conception this theory also has undergone some modifications, of which the most important is that put forward by du Toit (1937). Wegener (1924) postulated that all known land originally formed a single mass, which he termed ' Pangea ' and this was surrounded by a single ocean, ' Panthalassa '. A somewhat similar view was put forward by Williams (1931) ; but whereas Wegener placed his ' Pangea ' in the Equatorial region, Williams placed this originally single land mass at the South Pole. Du Toit (1937) considers that there were originally two great land masses, situated respectively at or near the North and South Poles.. The northern mass, known as Laurasia, included the mass of Arktis (North America) in the Western Hemisphere and Angaraland (Europe and Asia) in the Eastern, while the southern mass, termed Gondwanaland, included parts of South America, most of Africa, India, Australia and probably Antarctica (*vide* fig. 2).

Both theories admit that in the Mesozoic a wide sea, the Tethys, ran from east to west separating Laurasia in the north from Gondwanaland in the south, and connected the western and eastern parts of the Pacific Ocean ; both theories also agree that it was not until Cretaceous times that the present continents became finally and completed separated. According to the older theory large land masses, that had originally acted as ' bridges ', broke off and sank beneath the sea, a process that, according to the Theory of Isostasy and the results of recent investigations of the ocean floor, cannot possibly have taken place : the later theory of continental drift supposes that the two great masses of Laurasia and Gondwanaland broke up into several fragments and that these gradually drifted apart until they finally reached their present positions, a process that many geologists and geophysicists tell us is equally impossible. Biologists are thus left between the devil and the deep sea.

Personally I much prefer the later ' Drift Theory ' and in this Address I shall try to show that the facts of the geographical distribution of many of the Copepoda can best be explained by the drifting apart of the great land masses.

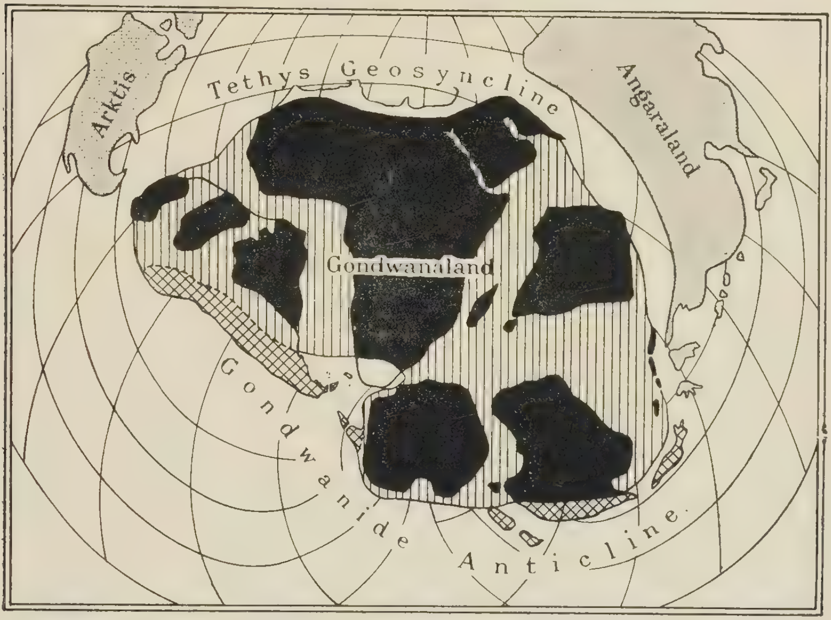

FIG. 2.—Gondwanaland in the Middle Palaeozoic Epoch according to du Toit's modification of the Continental Drift Theory.

Hitherto attention appears to have been paid mainly to the suggestion that the major line of drift was westwards, as was postulated by Wegener : but certain others and especially Taylor (1928) have suggested that the line of drift was brought about by the rotation of the earth and the resulting centrifugal force. If this force were the main factor in producing the drift, then surely each fragment of Gondwanaland and Laurasia would have travelled towards the Equator from its original position near the South or North Pole and the direction of drift would have approximated to the meridian of longitude that passed through the centre of gravity of each fragment, though, as the fragments moved northwards or southwards they might have been given a westward trend under the influence of the ' Coriolis ' force, comparable to that imparted to a mass of water flowing from south to north in the Southern Hemisphere or from north to south in the Northern Hemisphere : thus Arktis (North America) would have drifted first southwards and then south-westwards and South America would have moved northwards along a line approximating to the meridian of 65° W. ; Africa along the meridian of about 20° E. ; India along about 75° E. and Australia along approximately 135° E. (fig. 3). As this northward or southward movement continued the gap between two fragments would steadily become greater, thus giving rise to an apparent drift towards the west, until each fragment reached the position it occupies to-day. The drift of the fragments of Angaraland and Gondwanaland appears to have been of an intermittent character and to have been interrupted by occasional movements in the opposite direction, so that from time to time a connection was established and later interrupted between the northern and southern land masses. Wadia suggested that in the Middle Carboniferous " a continuous land bridge must have stretched from the Punjab (India) as far as the Pamir Plateau—possibly beyond " (*vide* Sahni, 1936, p. 720) and Wadia himself (1938, p. 94) remarks that " even during the Upper Carboniferous the Kashmir part of the Tethys must have been studded with an archipelago of volcanic islands ". Another bridge occurred during the Upper Jurassic in the Afghanistan region (du Toit, 1937, p. 171). Wadia (1937, p. 58) has pointed out that in India " the Cutch Jurassic fossils present no affinities with the Mediterranean or North-west European Province, but they show kinship to the Jurassic faunas of Madagascar. In another of these transgressions of the sea, the Trichinopoly coast was submerged and covered with some 3,000 feet of richly fossiliferous grits, sandstones and clays, in which are preserved more than 1,000 species of marine molluscs, the majority of them being ammonites, disclosing close relationship with the Cretaceous of Madagascar and Natal ". In a summary of a communication made by Fox (1937) during a discussion on " The Age of the Deccan Trap " held at the Meeting of the Indian Science Congress in Hyderabad, he states that " On the Madras coast there are Upper Gondwana strata with a Rajmahal flora, but including some marine fossils which were determined as Jurassic cephalopods. Recently these supposed Jurassic animal remains were re-examined by Dr. Spath who considers their previous identification an error. In his opinion the fossils appear to belong to the uppermost Jurassic or perhaps the lowest part of the Cretaceous ". It thus appears that about this period there was an isthmus connecting the northern part of Africa with northern India and separating the Tethys Sea from what is now the Arabian Sea. In the late Cretaceous the entrance to the Tethys Sea from the Pacific became blocked by the formation of a causeway between India and China and it was not until the Eocene that sinking " led to the re-establishment of

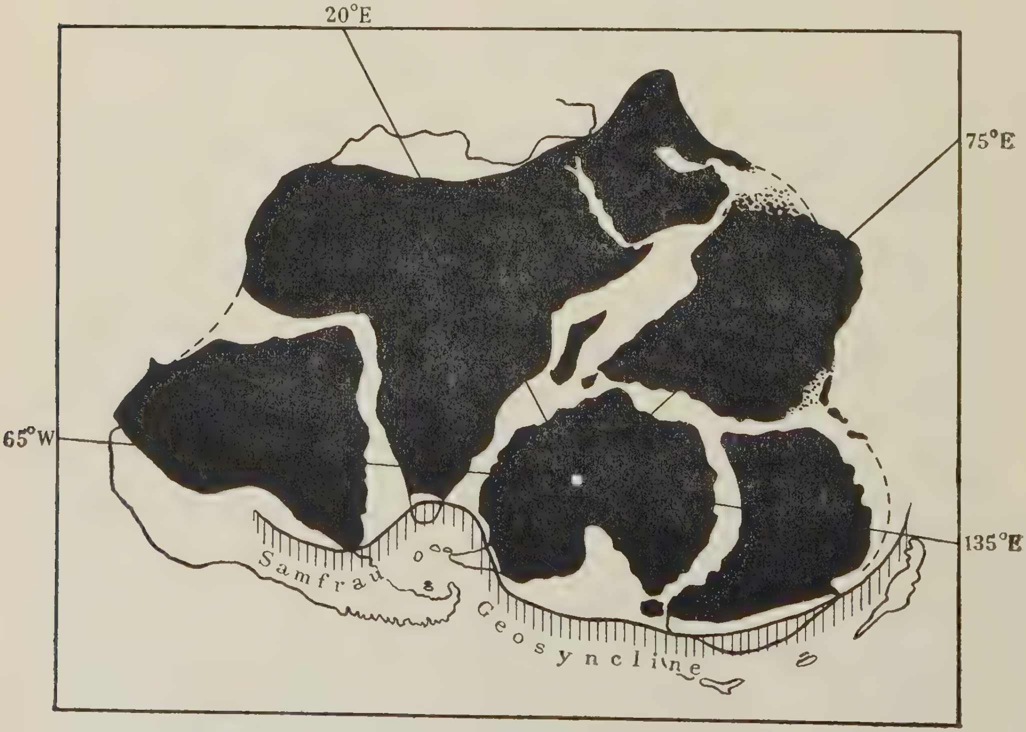

FIG. 3.—Gondwanaland in the Mesozoic Era, showing the suggested lines of drift of the fragments (after du Toit).

the Tethys between peninsular India, Tibet and China " (*vide* du Toit, p. 182). Towards the close of the Cretaceous the deposits of the Bagh beds in the Narbadda valley of India show " greater affinity with the Cretaceous of Arabia and Europe than with the adjacent Assam or Trichinopoly province. This dissimilarity shows that the two seas were still separated by some great and far-reaching barrier " (Wadia, 1937). It would thus appear that in the upper Cretaceous the bridge, that had joined India and Africa through Arabia in the Jurassic, had been breached, and so permitted the Tethys Sea fauna to invade the west coast of India while the faunas of the eastern side of India, occupying the Indo-Australian Gulf, were still isolated from the Indo-African gulf, presumably because the former gulf had not at that time penetrated sufficiently far to separate India from Antarctica, its western end still being blocked by Madagascar (*vide* fig. 13). In the Eocene and Miocene the upheaval of the Himalayas, which appeared to have commenced at the eastern end of the range, created a final block across the eastern end of the Tethys Sea, cutting it off completely from the Pacific.

It seems probable that along each line of fracture a condition must have arisen that was somewhat similar to that which is found to-day in the Great Rift Valley of Africa, which, it has been suggested, is a rift in the process of formation, and that a series of fresh-water lakes and rivers was formed in the line of fission and only at some time later did the sea encroach over the rift. According to du Toit, as early as the Ordovician a geosyncline ran round the southern part of Gondwanaland and to this he gave the name of the ' Samfrau ' Geosyncline. Camp (1952, p. 211, footnote) has remarked that " It seems quite probable that the Amazon is a reversed river, which once flowed westward. Those who delight in speculation on continental displacement might well wonder whether the Niger River could possibly be the headwaters of a once westward-flowing Afro-South American river system " ; and in his fig. 25 he shows South America as being composed of four land areas, of which the north and north-east three were parts of Gondwanaland, while the area on the west and south was probably a part of the Gondwanide anticline. Between these four areas he shows a sea-way that was open at least in part as late as the Miocene. Along the ' Samfrau ' Geosyncline the sea was gradually displaced and probably a chain of fresh-water lakes and in South America the great valley of the La Plata River were formed : outside this depression ran a Pregondwanide elevation that arose in the Carboniferous and eventually gave rise to the western margin of South America, the tip of South Africa and probably Grahamland in the Antarctic, while at its eastern end it formed New Zealand, New Caledonia and New Guinea, and possibly Timor ; Sahni has suggested that even Java and Sumatra may have once formed part of Gondwanaland. Finally, in the late Cretaceous, the eastern part of Gondwanaland broke up into islands and New Zealand and New Guinea drifted away into the Pacific, while Australia finally separated from Antarctica.

In an attempt to discover whether the present-day distribution of the Copepoda can best be explained by one or other of the two theories one's first difficulty lies in the question: When did this Group arise? No fossil remains of any Copepod have as yet been reported : the only known fossil that might be considered to be closely related to the Copepods, *Euthycarcinus kessleri* Handlirsch, dates from the Triassic, and remains of several small Crustacea included in the family Cyclidae Packard, which may perhaps be attributed to the Branchiura, have been recorded from the Carboniferous (*vide* Hopwood, 1925) : remains of the Ostracoda are well known and date from the Cambrian. It thus seems not improbable that the Copepoda also arose in a far distant geological epoch and there can be little doubt that they were at first marine in their habitat and only later invaded fresh water, and this invasion by members of all three of the great groups, Calanoida, Cyclopoida and Harpacticoida, is by most observers now recognized as having occurred in very ancient times, possibly as far back as the Triassic or even Pre-Cambrian (*vide* Arldt, 1917). If we are prepared to admit the probability that the three great families, the Diaptomidae of the Calanoida, the Cyclopidae of the Cyclopoida and the Canthocamptidae of the Harpacticoida, were in existence in the Triassic or perhaps a little later in the Jurassic, it seems clear that at that time owing to the continuity or contiguity of the great land masses, as is suggested by one or other of the geological theories, there was a relatively easy means of migration from one area to another. The subsequent separation of the continents, either by foundering of land bridges or by drifting, will have isolated the various colonies and thus have rendered possible the evolution of a number of genera and subgenera in each area. Kiefer (1932) made a careful study of the Diaptomidae of the Eastern Hemisphere and created a number of ' genera ' to accommodate the numerous species that up to then had been included in the genus *Diaptomus* and in a later paper (1939 a) he showed that these new genera fell into two groups, which he termed the ' Arctic ' and ' Gondwana ' groups, according to the region in which they occurred: in 1936 he erected several other ' genera ' to accommodate species from South America. Light (1944) added yet another group of ' genera ' (or subgenera as they are now considered) to accommodate the species found in South America; and Tafall (1943), Brehm (1950) and Wilson (1951) have added a few more. In the following table I have given the various subgenera that are known to occur in the different regions :—

LAURASIA		GONDWANALAND	
North America	Europe and Asia (Kiefer's ' Arctic ' Group)	Africa, India and Australia (Kiefer's ' Gondwana ' Group)	South America
Aglaodiaptomus	*Acanthodiaptomus*	*Allodiaptomus*	*Argyrodiaptomus*
Entrichodiaptomus	*Arctodiaptomus*	*Anadiaptomus*	*Calodiaptomus*
Hesperodiaptomus	*Diaptomus* s. str.	*Arctodiaptomus*	*Dactylodiaptomus*
Leptodiaptomus	*Eodiaptomus*	*Heliodiaptomus*	*Idiodiaptomus*
Mastigodiaptomus	*Eudiaptomus*	*Metadiaptomus*	*Notodiaptomus*
Microdiaptomus	*Heliadiaptomus*	*Neodiaptomus*	*Odontodiaptomus*
Nordodiaptomus	*Mixodiaptomus*	*Paradiaptomus*	*Rhacodiaptomus*
Onychodiaptomus	*Mongolodiaptomus*	*Phyllodiaptomus*	
Pelorodiaptomus	*Metadiaptomus*	*Sinodiaptomus*	
Prionodiaptomus	*Neodiaptomus*	*Thermodiaptomus*	
	Neutrodiaptomus	*Tropodiaptomus*	
	Nordodiaptomus		
	Sinodiaptomus		
	Heliadiaptomus		

We thus have at the present day 22 genera (or subgenera) in Laurasia, 10 in North America (Arktis) and 14 in Europe and Asia (Angaraland), one genus, *Nordodiaptomus*,* being common to both regions; the migration of this genus from one area to the other could have been accomplished by the bridge that connected the two regions as late as the Miocene. In Gondwanaland we have 11 genera in the region comprising Africa, India and Australia, and 7 in South America, but there is no overlap between these two areas across the South Atlantic (*vide* fig. 4).

Wright (1927, p. 101) called attention to the fact that " there is a large part of the continent (South America) in which *Diaptomus* has never been found. . . . This peculiar distribution of the Centropagidae is presumably related to the geological history of South America " and he suggests that perhaps the genus *Diaptomus* was unable to compete successfully with other genera in the Chilean region. There is, however, another possibility: as already mentioned, Camp (1952, p. 211, fig. 25) has suggested that the Gondwana portion of this continent was originally subdivided into three main areas and that between these and the western border of the continent that now forms Chile and Peru, there was a sea-way that was in existence as late as the Miocene, and this may have proved to be a barrier to the western migration of this genus. Between Angaraland and Gondwanaland we have four genera that are present in both areas, namely *Arctodiaptomus*, *Heliodiaptomus*, *Neodiaptomus* and *Sinodiaptomus*.* The related genus *Metadiaptomus* has also managed to migrate from Angaraland to Gondwanaland

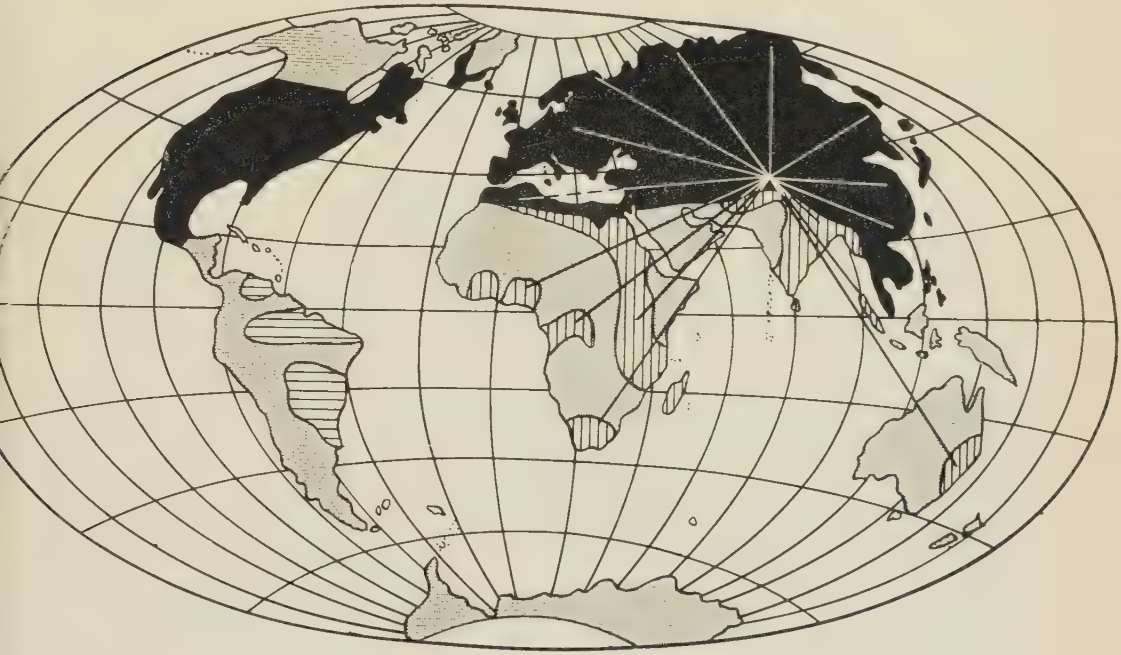

FIG. 4.—Distribution of the genus *Diaptomus* (s. lat.)
(after Tollinger (1911) and Kiefer (1932, p. 39).

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* In the subgenus *Nordodiaptomus*:
D. (*Nordodiaptomus*) *siberiensis* Wilson, in Siberia.
,, ,, *alaskaensis* Wilson, in Alaska.
In the subgenus *Arctodiaptomus*:
D. (*Arctodiaptomus*) *salinus* (Daday), throughout Laurasia and in Africa and India.
In the subgenus *Heliodiaptomus*:
D. (*Heliodiaptomus*) *nipponicus* (Kokubo), in Japan.
,, ,, *kikuchii* Kiefer, in Japan. (*Nom. nov.* for *D. viduus* non Gurney Kikuchi.)
,, ,, *contortus* Gurnay, in India.
,, ,, *viduus* Gurney, in India.
In the subgenus *Sinodiaptomus*:
D. (*Sinodiaptomus*) *chaffanjoni* (Richard), in China.
,, ,, *sarsi* (Rylov), in Manchuria.
,, ,, *indicus* Sewell, in India. (=*D. ganessa* Brehm.)
In the subgenus *Neodiaptomus*:
D. (*Neodiaptomus*) *schmackeri* (Poppe & Richard), in China and India. (=*D. strigilipes* Gurney.)
,, ,, *handeli* (Brehm), in China.

or *vice versa,* being represented in these two areas by the following species (*vide* Gurney, 1931) :—

In Angaraland :
Metadiaptomus asiaticus Daday.
,, *alluaudi* Guerne & Rich.
,, *chevreuxi* Guerne & Rich.

In Gondwanaland :
Metadiaptomus aethiopicus Daday.
,, *capensis* Sars.
,, *colonialis* Van Douwe.
,, *masculus* Brady.
,, *meridianus* Van Douwe.
,, *purcelli* Sars.
,, *rigidus* Sars.
,, *rehmanni* Grochm.
,, *transvaalensis* Methuen.

Migration from one area to the other could have been accomplished across any or all of the bridges that I have mentioned above (*vide supra,* p. 152) prior to the late Cretaceous, and at any time since the final disappearance of the eastern end of the Tethys Sea in the early Tertiary ; or from Europe to Northern Africa or vice versa during the Glacial Period, when the lowering of the water level in the Mediterranean Sea caused the appearance of land bridges across the Strait of Gibraltar or from Tunisia through Sicily to Italy (*vide* Sewell, 1948, p. 474, fig. 87).

Gurney (1931, pp. 18 *et seq.*) has pointed out that both the Cyclopoida and Harpacticoida contain cosmolopolitan genera and that a species of the genus *Cyclops* (s. lat.), *C.* (*Mesocyclops*) *leuckarti* (Claus), has a distribution that is almost world-wide and has evolved into subspecies in different parts of the globe, viz. *bodanicola* Kiefer in Europe, *aequatorialis* Kiefer in Equatorial Africa, *deccanensis* Lindberg in India and possibly *edax* (Forbes) in North America. Though Gurney points out that a wide distribution is not proof of anything more than extreme power of dispersal, he admits that " the universal occurrence of the genus *Cyclops* does indicate very ancient origin ", and that *Diaptomus* is also " a very ancient fresh-water genus ". Kiefer (1929) in a detailed study of the genera of the family Cyclopidae has grouped the species into a series of subgenera and later he (1939 a) has divided those of the Eastern Hemisphere into groups ' Arctic ' and ' Gondwana ' as in the Diaptomidae. In the table below I have given the distribution of the subgenera in the different regions :—

	LAURASIA		GONDWANALAND
	' Arktis ' N. American Group	' Angaraland ' ' Arctic ' Group of Kiefer	' Gondwana ' Group of Kiefer
Cyclops (s. lat.)	(1)	*Cyclops* (s. str.) (6)	
	(2)	(3)	*Microcyclops* (24)
	(1)	*Megacyclops* (3)	(1)
	(3)	*Acanthocyclops* (9)	(3)
	(4)	*Diacyclops* (22)	(4)
	(1)	(4)	*Metacyclops* (9)
	(2)	(4)	*Thermocyclops* (19)
	Orthocyclops (1)		
		Bryocyclops (4)	
	(1)	(1)	*Ectocyclops* (3)
	(2)	(4)	*Paracyclops* (4)

In the closely related genus *Euclops* we find the same wide distribution of the subgenera :—

Eucyclops (s. lat.) {		...... (7)	....*Eucyclops* (s. str.) (18)
	(1)........	...... (1)	....*Tropocyclops* (2)
	(3)........	*Macrocyclops* (3) .	...........(2)

In the above table the figure in brackets is the number of species that have been reported from the three great land areas. From the table it can be seen that the demarcation into groups in different areas is less sharply marked than in the Diaptomidae. Out of a total of 14 genera or subgenera as many as 10 have been recorded from all three regions, namely Arktis, Angaraland and Gondwanaland : *Orthocyclops* is known only from ' Arktis ' ; *Bryocyclops* is known only from Java which is by some regarded as part of Angaraland but may perhaps be a part of Gondwanaland ; and the subgenus *Eucyclops* is known only from Gondwanaland, and *Cyclops* (s. str.) only from Arktis and Angaraland.

In the Harpacticoida Chappuis (1933 a, b) has studied the distribution of the subfamily Canthocamptinae of the family Canthocamptidae (fig. 5) and he has shown that there are several genera and even species that have a wide distribution, some having been taken on both sides of the North Atlantic Ocean in ' Arktis ' and ' Angaraland ', while others have spread in the Southern Hemisphere between ' Angaraland ' and ' Gondwanaland ' or vice versa. In the table below I give the distribution of the various genera and subgenera of this subfamily :—

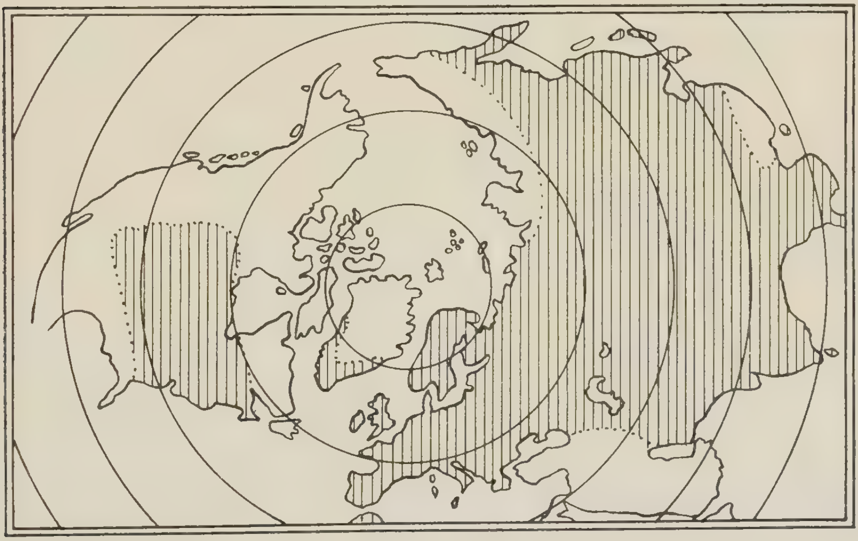

FIG. 5.—Distribution of the family Canthocamptidae shown on the map of Laurasia in the early Mesozoic Era (as reassembled by du Toit).

ARKTIS	ANGARALAND		GONDWANALAND
	Paracamptus	(1)	
	Ceuthonectes	(2)	
	Hypocamptus	(2)	
	Maraenobiotus	(7)	
(1)........	*Canthocamptus*	(4)	
(3)........	*Moraria*	(12)	
	Bryocamptus s. lat.		
(3)........	..*Bryocamptus* s. str.	(9)	
	Arcticocamptus	(8)	
	Attheyella s. lat.		
	Attheyella s. str.	(3)	
(3)........	..*Brehmiella*	(6)	
	Chappuisiella		.... (9)
	Delachauxiella		.... (13)
	Echinocamptus s. lat.		
	Echinocamptus s. str.	(3)..	.... (2)
(2)........	..*Limocamptus*	(6)	
(2)........	*Ellaphoidella*	(9)..	.... (13)
(1)........	*Epactophanes*	(2)..	.... (2)

The two genera *Canthocamptus* and *Moraria* have been able to spread westwards from Angaraland to Arktis (North America), and so has the subgenus *Bryocamptus* s. str. of the genus *Bryocamptus* s. lat. In the genus *Attheyella* one subgenus, *Brehmiella*, has developed in Arktis and *Chappuisiella* (fig. 6) appears to have developed in the Gonwanide anticline and have spread into Gondwanaland, occurring over the whole of S. America, Australia, New Guinea, and in Borneo, Java and Sumatra, while *Delachauxiella* is known from the western part of South America, in Peru, Chile, Argentina, Uruguay, and

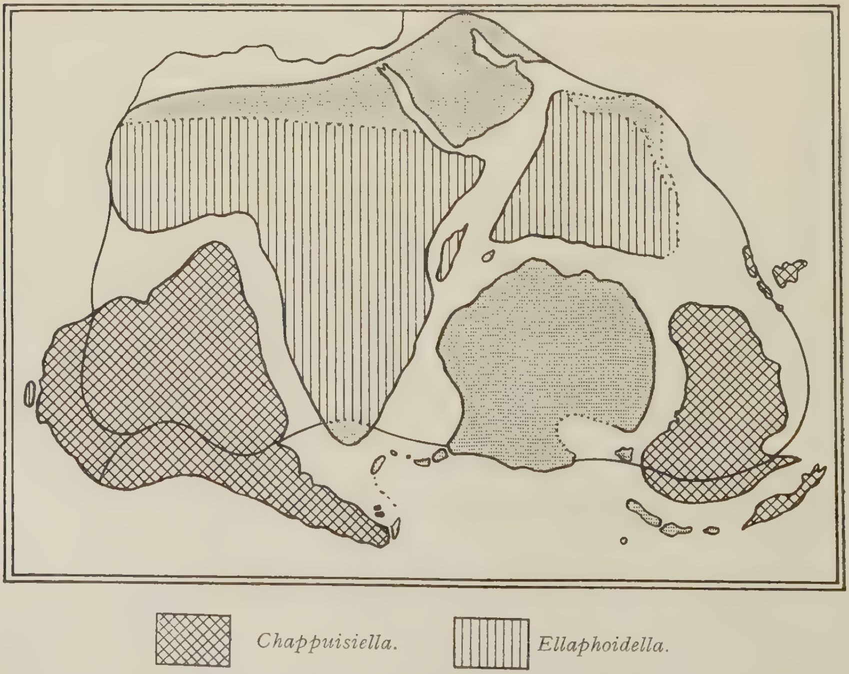

FIG. 6.—Distribution of the subgenus *Chappuisiella* Brehm of the genus *Attheyella* Brady and of the species *Ellaphoidella sewelli* Chappuis (from Chappuis, 1933).

Patagonia, the Falkland Isles and New Zealand. In the genus *Echinocamptus* one subgenus, *Echinocamptus* s. str., has managed to spread into Gondwanaland and a second, *Limocamptus*, has invaded Arktis (*vide* fig. 7) ; finally *Ellaphoidella* appears to have originated in Gondwanaland and has spread into both Angaraland and Arktis, and *Epactophanes* also occurs in all three regions.

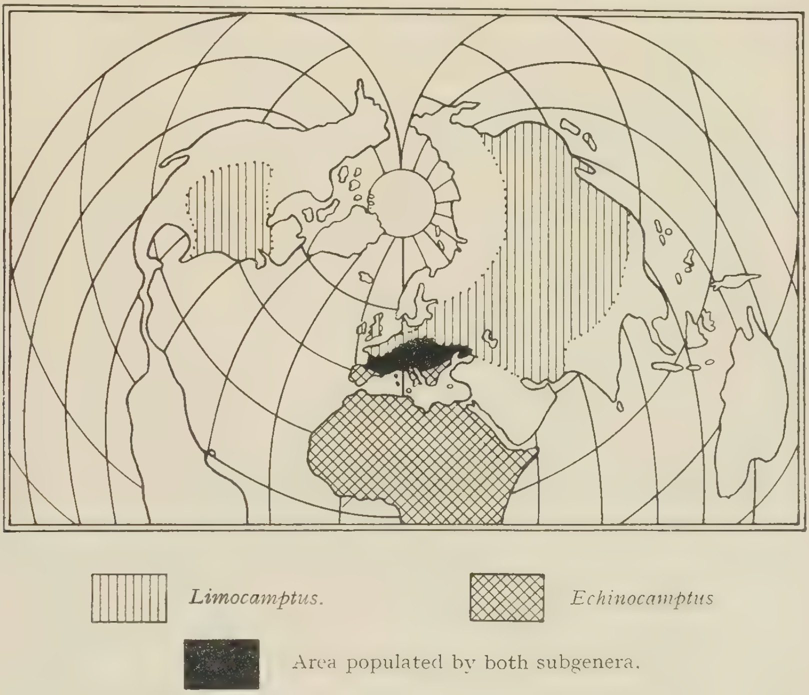

FIG. 7.—Distribution of the subgenera *Limocamptus* Chappuis and *Echinocamptus* Chappuis of the genus *Echinocamptus* Chappuis, subfamily Canthocamptinae (from Chappuis, 1933).

In some genera even a species has been able to spread widely with the evolution of subspecies in different regions. *Bryocamptus* (*Bryocamptus*) *minutus* (Claus) has been reported as subspecies *minutus* s. str. over Laurasia and as subspecies *minnesotensis* (Herrick) in Arktis. In the genus *Attheyella* subgenus *Brehmiella* s. str., *A.* (*Brehmiella*) *northumbrica* Brady has several subspecies in Angaraland and one, *americana* (Herrick), in Arktis. In the genus *Ellaphoidella* three species have a wide distribution: *E. sewelli* Chappuis (fig. 6) extends from islands off the north coast of South America, where the subspecies *americana* Chappuis has been reported from the island of Bonaire off Venezuela, other subspecies *occidentalis* Chappuis and *africana* Chappuis occur in Africa, *sewelli* Chappuis and *indica* Chappuis are present in India in the eastern Himalayan region, and *eremita* Chappuis occurs in Assam ; it thus occurs across the whole width of Gondwanaland (*vide* fig. 6), while further east we have a very close relation in *E. malayica* Chappuis in Java ; *Ellaphoidella bidens* (Schmeil) has one subspecies, *bidens* s. str., that occurs in Laurasia, Arktis and Gondwanaland and a second, *coronata* (Sars) that has been reported from Gondwanaland and from Arktis ; and *E. grandidieri* (Guerne & Richard) occurs in both North and South America and in Africa, Madagascar, Ceylon, Malay Archipelago, Indo-China, Java, China, New Guinea and the Hawaiian Islands.

Thus in all three groups we have evidence that points to a very considerable dispersal and probably to a great antiquity. Tollinger (1911) and Burckhardt (1913) were both of the opinion that migration into fresh water reached its maximum in the middle of the Tertiary, but that the Diaptomidae had been able to emigrate from Africa to South America at a much earlier date, and Tollinger suggests that this migration took place in the Cretaceous, when a connection existed between these two areas.

The possession of a pair of grasping antennules in the males of the Cyclopoida and Harpacticoida, whereas there is either only one or none at all in the Calanoida, has been put forward as an argument that the first two groups are more primitive and presumably older than the last; Gurney (1931, p. 82) remarks that " There can be very little doubt that both antennules were primitively prehensile in the male, and that the unmodified antennule of the Calanidae is secondary ". The distribution of the various subgenera and even of species, with in some cases the evolution of subspecies in different regions in both the Cyclopidae and Canthocamptidae, in contrast with the relative infrequency of a subgenus and still more of a species in more than one geographical area in the Diaptomidae, suggests that these two groups were able to extend their distribution at a somewhat earlier date or else that their rate of evolution was more rapid than in the Diaptomidae. Possibly both factors may have been responsible. It further suggests that not very long after the Diaptomidae had managed to migrate from one area to another as, for instance, from Africa to South America in Gondwanaland or from Laurasia to Arktis in the Northern Hemisphere, dispersal from one area to another has been either infrequent or even impossible, except where later earth movements caused the fusion of one land mass with another, as in the Indo-Chinese region, or, relatively recently, by the appearance of land bridges across the Mediterranean Sea during the last Glacial period (*vide* Sewell, 1948).

Brehm (1936), in his study of the circum-antarctic distribution of the fresh-water fauna, called attention to the very interesting distribution of the family Boeckellidae, and especially of the two genera *Boeckella* Guerne & Richard and *Pseudoboeckella* Mrázek; and of these Marsh (1924) considers the latter the more primitive. The genus *Pseudoboeckella** includes some 12 species and has a range that includes Peru, Chile and Patagonia in South America with an extension to the Falkland Islands, South Georgia and Grahamland in the Antarctic, and to Kerguelen. *Boeckella*,† on the other

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* Species of the genus *Pseudoboeckella* Mrázek:

1. *poppei* Mrázek ..	Patagonia and South Georgia.
2. *klutei* Brehm ..	El Junco—40° S.
3. *braziliensis* Lubb ..	Patagonia and Tierra del Fuego.
4. *dubia* Daday ..	Patagonia.
5. *silvestrii* Daday ..	Patagonia.
6. *entzi* Daday ..	Patagonia, Tierra del Fuego, South Georgia and Ludwig Philippe Island.
7. *longicauda* Daday ..	Patagonia.
8. *erubescens* Brehm ..	Chile—33° S.
9. *valentinii* Scott ..	Falkland Islands.
10. *gibbosa* Brehm ..	Chile.
11. *brevicaudata* Mrázek	Patagonia, Falkland Islands and Kerguelen.

Species of the genus *Boeckella* Guerne & Richard:
Western Group.

1. *bergi* Richard	From La Plata southwards to 50° S.
2. *occidentalis* Marsh	Peru, Bolivia.
3. *gracilis* Daday	Patagonia.
4. *poopoensis* Marsh	Bolivia.
5. *gracilipes* Daday	Peru, Chile, Patagonia.
6. *michaelsoni* Mrázek (=*pygmaea* Daday, *andersonorum* Ekman)	Patagonia, Falkland Islands, South Georgia.
7. *rahmi* Brehm	Chile.

hand, appears to have a discontinuous distribution; the western group, comprising some 10 species, occurs from Peru and Bolivia through Chile with an offshoot to the extreme southern end of Brazil in the La Plata river, Patagonia, the Falkland Islands and South Georgia; the eastern group, comprising some 22 species, occurs in Tasmania, Australia (Victoria, New South Wales, South Australia and Western Australia) and in New Zealand, while a single species has been recorded as far north as Mongolia. Two species of the genus *Boeckella* are known from Lake Titicaca on the Peru-Bolivian border and the presence in Mongolia of the species *orientalis* led Brehm to suggest that perhaps the genus has migrated southwards and that these species were dropped and left behind during the migration: but Marsh (1924, p. 27) thinks that the genus originated in the Antarctic continent and that the various species became differentiated in different localities, and Fairbridge (1945) agrees with this view and concludes that the close affinity between the species that he described from Western Australia and that from Mongolia points to the migration having been towards the north and not from it. Other closely related genera occur in parts of the same area, thus *Parabroteus* Mrázek, represented by a single species *michaelsoni* Mrázek, occurs in South Patagonia, the Falkland Islands and South Georgia; and at the other end of the region we have *Hemiboeckella* Sars with a single species, *searli* Sars, in East Australia, and *Metaboeckella* Sars, also with a single species, *dilatata* Sars, in New Zealand.

That at one time the islands of New Zealand were much more closely connected with Australia is, as Brehm (1936) has pointed out, strongly suggested by the distribution of the genus *Gladioferens* Henry, in which seven species are known from the coastal waters of New Zealand and South Australia and

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8. *dentifera* Brehm	Chile.
9. *meteoris* Kiefer	Patagonia.
10. *schwabei* Brehm	Chile.
11. *godeti* (Delachaux)	Peru.
Eastern Group.	
1. *triarticulatus* Thoms.	South-east Australia, New Zealand.
2. *oblonga* Sars	Victoria, South Australia.
3. *saycei* Sars	Victoria, South Australia.
4. *symmetrica* Sars	Victoria, South Australia.
5. *robusta* Sars	New South Wales.
6. *minuta* Sars	Victoria, New South Wales.
7. *propinquus* Sars (?=*triarticulata* Thoms.)	New Zealand.
8. *asymmetrica* Searle	Victoria.
9. *coronaria* Henry	New South Wales.
10. *fluvialis* Henry	New South Wales.
11. *insignis* Smith	Tasmania.
12. *longiseta* Smith	Tasmania.
13. *nyoraensis* Searle	Victoria.
14. *pseudocheles* Searle	Victoria.
15. *rubra* Smith	Tasmania.
16. *tenera* Sars	Victoria, South Australia.
17. *hamata* Brehm	New Zealand.
18. *ambigua* Percival	New Zealand.
19. *opaqua* Fairbridge	Western Australia.
20. *pellucida* Fairbridge	Western Australia.
21. *lacuna* Fairbridge	Western Australia.
22. *orientalis* Marsh	Mongolia.

Since the above lists were compiled Harding (1955) has added the following species from the Lake Titicaca region:—

Pseudoboeckella Mrázek:
12. *calcaris* Harding.
13. *palustris* Harding.
Boeckella Guerne & Richard:
Western Group.
12. *camjatae* Harding.
13. *titicacae* Harding.

from fresh water in New Zealand and New South Wales, with a single species in brackish water in Western Australia,* and also by the genus *Calamoecia* Sars, in which we have a single species, *australica* Sars, in New South Wales and another, *lucasi* Brady, in the north island of New Zealand.

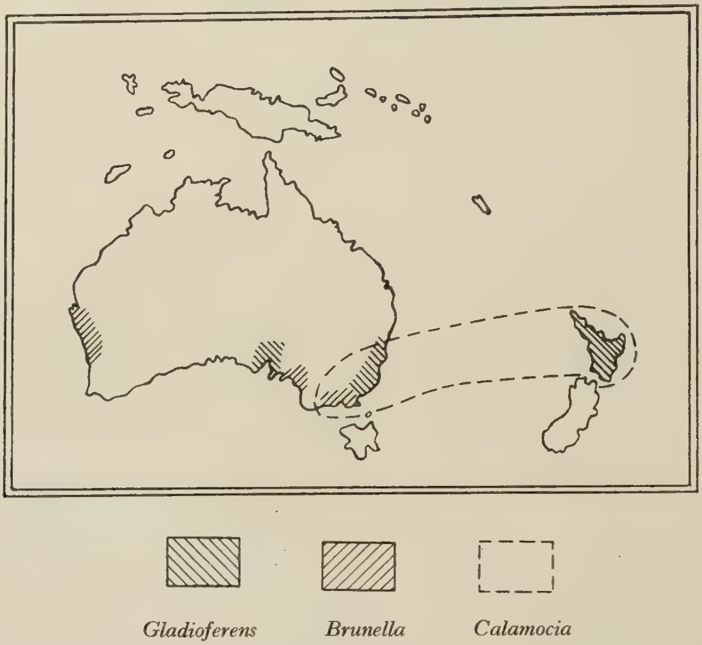

FIG. 8.—The present-day distribution of the genera *Gladioferens* Henry, *Brunella* Smith and *Calamoecia* Sars.

Brehm (1936, p. 491, fig. 8) has given a chart showing the circum-antarctic distribution of some of the fauna, among which he indicates that of the genus *Antarctobiotus* Chappuis, and of the species *Laophonte chathamensis* Sars and *Tigriopus angulatus* Lang. This last species has, in addition to its occurrence in the Antarctic, been reported from the Chilean Cordilleras by Brehm (1935) and from Abyssinia at a height of 2,300 m. by Chappuis (1935) : both these localities are situated in regions that were originally, according to the Continental Drift Theory, parts of Gondwanaland or the Gondwanide anticline. Brehm suggests that its occurrence in Abyssinia may have been connected with the migration of birds and this would have been much more easily accomplished during the late Jurassic or early Cretaceous, while South America and Africa were connected, than in later times after their separation had taken place.

I have taken the liberty of reproducing Brehm's chart with certain modifications and additions derived from the work of Lang (1933, 1934, 1935 and 1936) (fig. 8). Lang recorded from Macquarie and Campbell Islands, that lie on the submarine ridge connecting New Zealand with Antarctica, several

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* Species of the genus *Gladioferens* Henry :

1. *pectinatus* Brady .. Coastal waters, New Zealand.
2. *inermis* Nicholls .. Coastal waters, South Australia.
3. *brevicornis* Henry .. Coastal and fresh-water, New South Wales.
4. *imparipes* Thomson.. Brackish water, West Australia.
5. *gracilis* Kiefer .. Fresh water, New Zealand.
6. *subsalaria* Percival .. Fresh water, New Zealand.
7. *spinosus* Henry .. Fresh water, New South Wales.

Nicholls (1944, p. 2) suggests that *brevicornis* and *pectinatus* may be synonyms and that *subsalaria* is not really distinct from *brevicornis*.

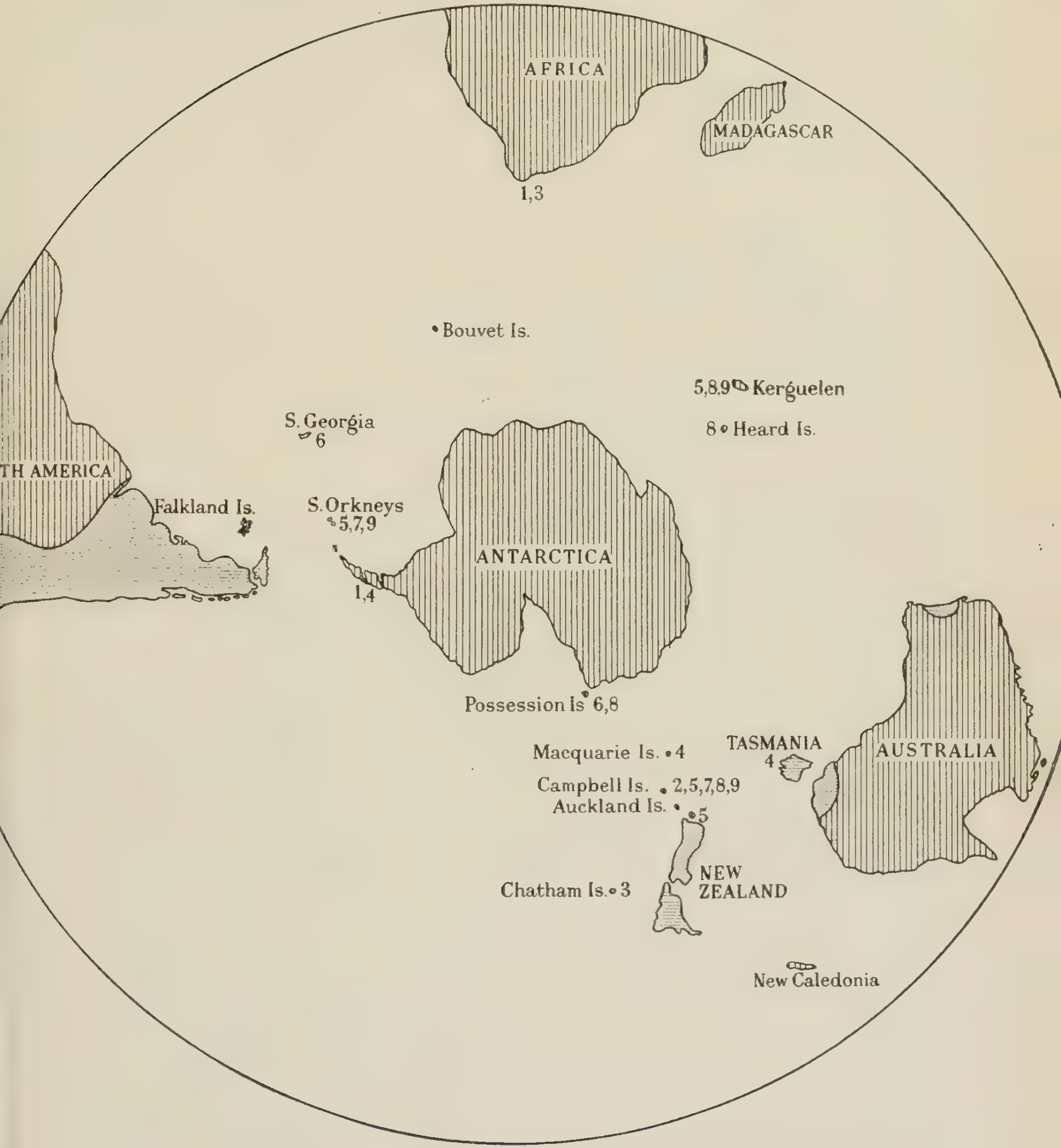

Fig. 9.—Showing the present-day distribution of certain species and genera of the circum-Antarctic region.

▨ *Boeckella* Guerne & Richard.

1. Genus *Zanclopus* Calman. 2. Genus *Perissocope* Brady. 3. *Laophonte chathamensis* Sars. 4. *Tigriopus angulatus* Lang. 5. *Harpacticus pulvinatus* Brady. 6. Genus *Antarctobiotus* Chappuis. 7. *Laophontodes whatsoni* T. Scott. 8. *Epactophanes antarcticus* (Richard). 9. *Diarthrodes imbricatus* (Brady).

species that were previously known from far distant parts of the Antarctic, as well as recording new species belonging to genera already known from species taken in distant areas. In fig. 9 I have indicated the distribution of eight genera or species of Harpacticids and one genus of a Notodelphyoid, *Zanclopus*, and in a footnote* below I give the recorded distribution of these and certain other examples.

In addition to the above species mention may also be made of the species *Mesochra nana* Brady, that has been reported from the Falkland Islands and Kerguelen and has also been taken in the Chilka Lake in India.

The genus *Godetella* Del. (=*Cletocamptus* Schmank.) also exhibits a widely discontinuous distribution : one species *kumleri* Del. has been described from a lake at a height of 5,140 m. in Peru, *deitersi* (Rich.) occurs in Patagonia and the Argentine, and perhaps *brehmi* Kiefer, which was taken in Guatemala and *bermudae* Willey taken in Bermuda are synonymous with *deitersi* : *trichotus* Kiefer was taken in South Africa. This last distribution suggests the presence of a connection between South America and South Africa.

The discontinuous distribution of these various genera and species would be very difficult to explain on the old theory of the Permanence of the Ocean Basins : but if we plot their distribution on a chart that shows the positions of the land masses during the Palaeozoic and early Mesozoic, as suggested by the Drift Theory (fig. 10), we see at once that in almost every case the present-day distribution lies close to the line of the ‘ Samfrau ’ geosyncline and the Gondwanide anticline. The fresh-water Calanoids and Harpacticids could easily have migrated from west to east, or vice versa, along the chain of lakes and rivers that presumably would have been formed as the Samfrau geosyncline gradually became silted up, while the marine Notodelphyoid and the Harpacticids could have migrated along the seaward side of the Gondwanide anticline (*vide* fig. 7) and have been subsequently carried to their present positions by post-Cretaceous drifting of the various land masses. In certain instances migration from island to island, as for instance from the Falkland Islands to Kerguelen may have been assisted or perhaps even have been brought about by coastal currents, but unfortunately we have at present no knowledge of how the currents ran in those far distant times.

In a consideration of the distribution of the marine surface-frequenting Copepoda we are faced with the fact that as soon as the present-day circulation of the surface water became established any planktonic form could be swept passively from one ocean to another or from one part to another of the same ocean, the only obvious difficulty in their survival being the changes of temperature that occur along the various convergence zones and more particularly in the region of the admixture of water from different sources off

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* Examples of discontinuous distribution of certain genera and species in the Antarctic :

1.	Genus *Zanclopus* Calman	South Africa and Grahamland.
2.	Genus *Perissocope* Brady	Campbell Is. and Antarctica.
3.	*Laophonte chathamensis* Sars	Chatham Is. and S. Africa.
4.	*Tigriopus angulatus* Lang	Tasmania, Macquarie Is., Grahamland.
5.	*Harpacticus pulvinatus* Brady ..	
6.	Genus *Antarctobiotus* Chappuis ..	Possession Is., South Georgia.
7.	*Laophontodes whatsoni* T. Scott ..	Campbell Is. and S. Orkneys.
8.	*Epactophanes antarcticus* (Richters) ..	Possession Is., Kerguelen and Heard Is.
9.	*Diarthrodes imbricatus* (Brady) ..	Campbell Is., S. Orkneys and Kerguelen.

Other examples of the same type of distribution are :

	Parawestwoodia assimilis Sars var. *antarcticus* T. Scott	Campbell Is. and S. Orkneys.
	Parastenhelia gracilis Brady .. (*P. antarctica* T. Scott)	Falkland Is., S. Orkneys and Kerguelen.
	Laophonte gracilis Brady	Falkland Is. and Kerguelen.
	Phyllopodopsyllus mossmani T. Scott	Falkland Is.
and	*Phyllopodopsyllus paramossmani* Lang	Stewart Is., New Zealand.

South Africa (*vide* Sewell, 1948). In this previous paper I suggested that the present fauna of the tropical and temperate regions of the North Atlantic was largely derived from the Pacific Ocean through the Tethys Sea, but that when this sea was cut off from the Pacific by the formation of the land connection between India and Asia in the Cretaceous the altered conditions in the Atlantic resulted in a marked change in the fauna and some 70 Indo-Pacific species eventually disappeared from the area that is now the Mediterranean Sea. Of these 70 species that are still found in the Atlantic Ocean, 44 are restricted, so far as we know at present, to the tropical and temperate regions of the North Atlantic, while the other 26 species are so far known only from the South Atlantic: this suggests that while originally these 44 North Atlantic species had been transported westwards through the Tethys Sea, the other 26 forms, that are at present confined to the South Atlantic, may have been brought there subsequently through a different route, namely, across the Indian Ocean and then round South Africa by the surface currents, when these became established after the breaking up of Gondwanaland and the drifting apart of the various fragments in the early Tertiary.

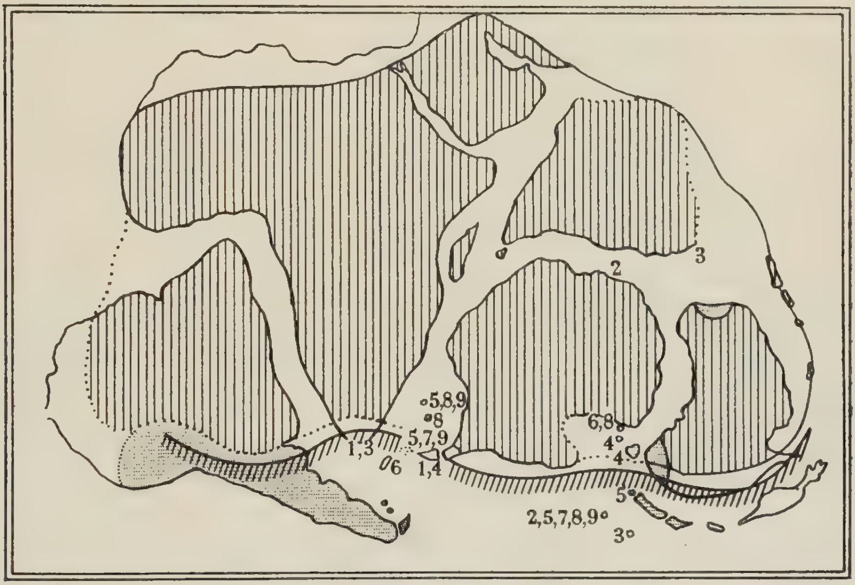

FIG. 10.—The same distribution plotted on the map of Gondwanaland in the Mesozoic Era according to du Toit. (The numbers refer to the same species as in fig. 9.)

Brehm (1926–27, p. 478) expected that the continental drifting envisaged in the Drift Theory would throw light on the geographical distribution of the coastal Copepoda and he suggested that the littoral species might merely have clung to their original habitats and so have become separated subsequently by wide oceans. Steuer (1933, p. 280), however, was opposed to this view and remarks that in the Atlantic Ocean at any rate not one of the strictly neritic species has its counterpart on the opposite coast. In a previous paper (Sewell, 1948) I have called attention to the difficulty experienced in attempting to draw any hard and fast line between the 'neritic' and 'oceanic' species in the planktonic Copepoda, but a consideration of the truly littoral or continental shelf inhabitants reveals some very interesting instances of species or genera that are at the present time known only from the two sides of the North Atlantic. One very good example of such a distribution is to be found in the genus *Platycopia* Sars: Sars (1921) originally described two species belonging to this genus from the southern coast of Norway, namely *P. perplexa* Sars and *P. pygmaea* Sars, from mud or muddy sand at depths of 60 and 30 fathoms respectively; and Wilson (1946) has recorded two other species, namely *P. tumida* (C. B. Wilson) and *P. sarsi* M. S. Wilson, both from a tidal pool on Mount Desert Island, Maine, on the North American coast. She also shows that these four species can be separated into two groups, each of which has a species from Norway and America, namely a *perplexa-sarsi* group and a *pygmaea-tumida* group. Among the Harpacticoida a number of littoral species have been recorded from habitats on the two sides of the North Atlantic.

(1) Species at present only known from the coast of Norway and the Woods Hole region of the Atlantic coast of North America :—

Amphiascus attenuatus Sars.
,, *obscurus* Sars.
,, *pallidus* Sars.
,, *sinuatus* Sars.
Laophonte proxima Sars.

(2) Species at present known from the coast of Norway, the British Isles and the Woods Hole area, with in a few cases a record from Heligoland :

Pseudothalestris pygmaea (T. Scott).
Amphiascus longirostris (Claus).
,, *intermedius* (T. Scott).
,, *parvus* Sars.
Stenhelia reflexa (Brady).
Ameira simplex (Norman & T. Scott).
,, *tenuicornis* T. Scott.
Leptastacus macronyx (T. Scott).
Evansula incerta (T. Scott).
Stenocaris minor (T. Scott).

One other species *Thalestris gibba* (Krøyer) is known from these areas and in addition from the coasts of Finland and Franz Joseph Land.

There is a possibility that all these species, like so many of the epiplanktonic forms may have been swept in relatively recent times across the North Atlantic Ocean by the Gulf Stream and its continuation the North Atlantic Drift and so have reached the British Isles and Norway, but they may also have been able to spread in earlier times from one region to another if, as is envisaged by the Drift Theory, these areas were in close proximity on either side of the North Atlantic rift when Laurasia began to break up.

A review of those species belonging to the warm-water marine planktonic genera that have been able to adapt themselves to a brackish or even a freshwater habitat reveals some very suggestive results. I have been able to compile records of 106 such species (*vide* Appendix I), but the numbers in each of the three great oceans exhibit considerable differences: in the Pacific Ocean 37 such species have been recorded, in the Indian Ocean 80, and in the Atlantic 54. Doubtless the invasion of brackish-water habitats from the sea is going on to-day in suitable localities, such as the estuarine regions of the great rivers and in areas like the Baltic Sea; and in all such regions marine species may be swept in by surface currents and so be taken in an area that is not yet their true habitat; among such species we find in the Baltic Sea :

Nannocalanus minor (Claus);
Temora longicornis (O.F.M.);
Acartia (*Acartiura*) *longiremis* (Lillj.);
,, (*Acanthacartia*) *tonsa* Dana;
Oithona similis Claus; and
Microsetella norvegica (Boeck);

all of which are warm-water species from the Indo-Pacific region.

Among the species that have been able to adapt themselves to a brackish-water habitat in the Indian and Atlantic Oceans is *Paracalanus crassirostris* Dahl, that has evolved into several subspecies or forms in different localities, namely :

f. *sewelli* Früchtl (≐*P. dubia* Sewell) in the Gangetic delta.
f. *scotti* Früchtl (=*P. pygmaeus* non. Claus, T. Scott) in the Congo estuary.
f. *typica* Dahl in the Amazon estuary.
f. *nudus* Davis in Chesapeake Bay in the North Atlantic.

Another case in which development has proceeded far enough to give rise to different species is found in the genus *Labidocera* Lubb. The species of this genus can be divided into two groups according to the number of segments in the abdomen of the female. In one group there are three segments and the species in this are also characterized by the absence of lateral hooks on the margin of the head and a tendency to the reduction of the endopod of the 5th leg in the female : *Labidocera euchaeta* Giesbrecht occurs in the western Pacific and in the Bay of Bengal in several of the estuaries ; *L. gangetica* Sewell occurs in the Gangetic delta ; *L. brunescens* (Czern.) is present in the Black Sea and the eastern end of the Mediterranean Sea ; *L. scotti* Giesbr. (=*L. darwini* T. Scott) is reported from the Congo estuary ; and *L. fluviatilis* Dahl from the Amazon estuary. This last species, however, differs from the others in possessing only two segments in the female abdomen.

The difference in the numbers of marine species that have become adapted to brackish-water conditions in the great oceans may to some extent be due to the number of great rivers that open into each area : but there may also be another factor, namely the conditions that were present in the Indian and Atlantic Oceans when they first came into existence : according to the Drift Theory, as the great land masses, Laurasia and Gondwanaland, cracked and began to drift apart, the line of fracture would at first, as I have already mentioned, in all probability be occupied by lakes and rivers, and as separation began the sea must have invaded the seaward end of the fracture ; but as the rift increased, the water in its upper reaches will still have been brackish, especially in the surface stratum, while at the extreme tip it will have been filled with almost pure fresh water. That one is justified in assuming this is indicated by the conditions that have been shown to have existed in other epicontinental seas : as du Toit (1937, p. 172) has pointed out, " in the related interior depression (in North America) the waters from the Tethys invaded Mexico, Texas and Arizona during the Comanchean (Lower Cretaceous), depositing limestones and marls with a Mediterranean fauna. . . . Marine conditions spread later to Wyoming with a fresh-water facies—' Kootenay '—beyond in the trough that extends northwards into Canada ". Similarly in the Indo-Assam region sinking in the Eocene again opened up the connection between the Tethys Sea and the Pacific Ocean and here too we find deposits of estuarine and fluviatile sediments, which, as du Toit remarks, recall the similar deposits of Upper Cretaceous times in the same area. Thus conditions in these rifts must have been very favourable for the invasion of brackish water by marine species, sufficiently so to account for the increased number of brackish- and fresh-water species in these two areas, Indian and Atlantic.

One of the best examples of the spread of a marine genus into brackish- and finally fresh-water habitats and the subsequent evolution of new species is to be found in the genus *Pseudodiaptomus* Herrick (s. lat.), the original home of which was without much doubt the western side of the Pacific Ocean. Marsh (1933) later subdivided this genus into two subgenera, *Pseudodiaptomus* (s. str.) and *Schmackeria* Marsh, while Johnson (1938) erected a third subgenus, *Pseudodiaptallous*, to accommodate a single species, *euryhyalinus*, taken off the west coast of North America. As Stillman Wright (1936) has pointed out,

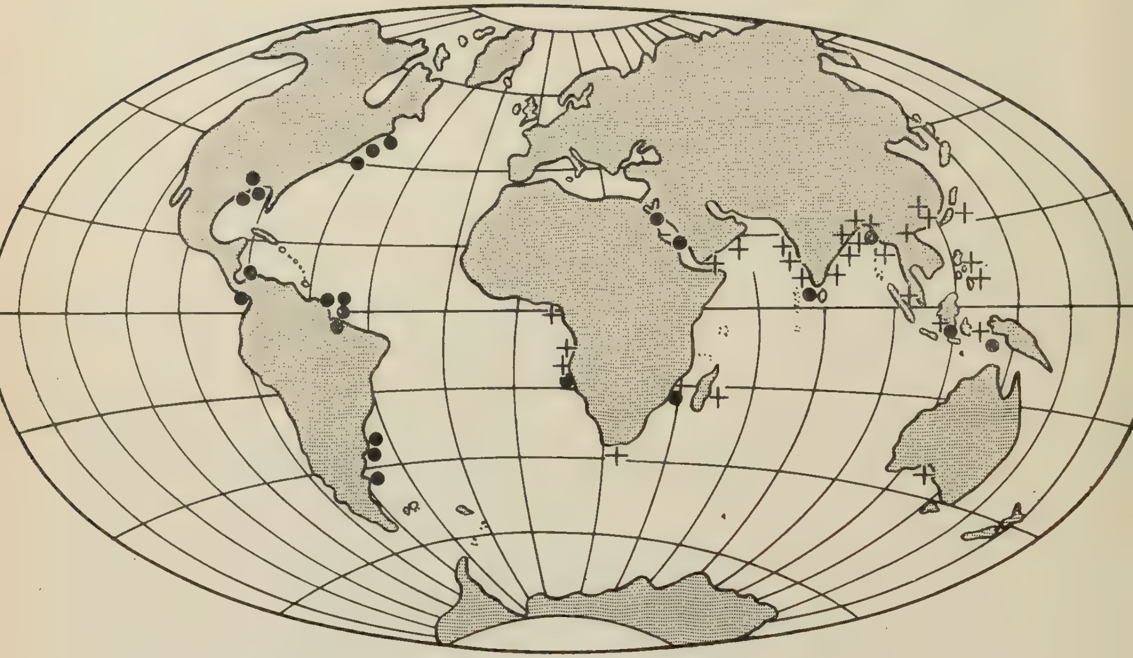

FIG. 11.—World distribution of the species of the two subgenera *Pseudodiaptomus* (s. str.) and *Schmackeria* of the genus *Pseudodiaptomus* (s. lat.).
● *Pseudodiaptomus* (s. str.). + *Schmackeria*.

all the species that occur in the Atlantic Ocean, with the single exception of the species *Schmackeria serricaudatus* T. Scott, which is present on the west coast of Africa, belong to the subgenus *Pseudodiaptomus** ; and he suggests

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* Species of the genus *Pseudodiaptomus* Herrick :

Subgenus *Pseudodiaptomus* Herrick :

Marine species.

P. (*Pseudodiaptomus*) *clevei* Früchtl	Aru Archipelago and Mergui Archipelago.
,, ,, *marinus* Brodski	Japanese waters.
,, ,, *salinus* (Giesbrecht)	Indian Ocean.

Marine and brackish-water species.

P. (*Pseudodiaptomus*) *aurivillii* Cleve	Malay Archipelago and Hooghli river.
,, ,, *cristobalensis* Marsh	North side of Panama Isthmus.
,, ,, *coronatus* Williams	East coast of North America.
,, ,, *hickmani* Sewell	Burma coast and Chilka Lake.
,, ,, *mertoni* Früchtl	Aru Archipelago and Kurau river, Perak.

Brackish-water species.

P. (*Pseudodiaptomus*) *acutus* (Dahl)	Amazon river estuary.
,, ,, *americanus* Wright	Mississippi river estuary.
,, ,, *culebrensis* Marsh	South side of Panama Isthmus.
,, ,, *gracilis* (Dahl)	Amazon river estuary.
,, ,, *hessei* Mrázek	Congo river estuary.
,, ,, *marshi* Wright	Estuaries of Rio Capibaribe and Rio Jaguaribe and Bahía de São Marco.
,, ,, *pelagicus* Herrick	Mississippi river estuary.
,, ,, *richardi* (Dahl) var. *inaequalis* Brian	Amazon, La Plata and Paraná river estuaries.
,, ,, *stuhlmanni* (Poppe & Richard)	Quilimane river estuary.

that the Atlantic species were all derived from a single ancestral form that subsequently divided into two: from one branch were derived *coronatus* Williams, *americanus* Wright, *pelagicus* Herrick, *acutus* (Dahl) and *richardi* (Dahl); while from the second branch sprang *marshi* Wright and *culebrensis* Marsh. He points out that the more primitive species, that in all probability closely resemble the ancestral form, occur in the North Atlantic and especially round the estuary of the Mississippi River, and he remarks, " it is becoming increasingly evident that the key to the problem of the origin and dispersal of the species of the Western Hemisphere, and perhaps of the genus as a whole, is to be sought in the region between the equator and latitude 30° N.'', that is, in exactly that area of the American coast against which the western end of the Tethys Sea impinged. He also suggests that the species *culebrensis* Marsh made its way westwards, from the Atlantic to the position that it now occupies, before the two Americas, North and South, became united by the Panama Isthmus in the Cretaceous. Another group of three species of *Pseudodiaptomus* (s. str.), namely *salinus* (Giesbrecht), *stuhlmanni* (Poppe & Richard) and *hessei* (Mrázek), occurs round the African coasts, the first two on the east side and the last on the west: *salinus* off the Arabian coast and in the Red Sea, *stuhlmanni* in the Quilimana estuary and *hessei* in the Congo estuary.

The subgenus *Schmackeria* Marsh* has spread widely along the Pacific coast of East Asia and a number of species have penetrated into fresh water; others have reached the region of the Bay of Bengal and the Andaman Sea and are now found in brackish water, only one, *lobipes* Gurney, having reached fresh water.

Burckhardt (1913) has pointed out that the majority of these species belong to a single group, in which he places *inopinus* Burckhardt, *forbesi* (Poppe & Richard), *poppei* Stingelin and *lobipes* Gurney: Wright (1937) has added *smithi* Wright. *Binghami* Sewell stands near to *lobipes* Gurney, and *tollingerae* Sewell near *poppei* Stingelin. The three species *annandalei* Sewell, *nostradamus* Brehm and *dubius* Kiefer are closely related and may have been derived from a single ancestor that belonged to Burckhardt's group. Two other species of *Pseudodiaptomus* (s. lat.), namely *burckhardti* Sewell and *masoni* Sewell, have been taken in the Andaman and Nicobar region and are marine in their habitat, but they cannot at present be placed in either subgenus as the males are unknown.

* Subgenus *Schmackeria* Marsh:

Marine species.

P. (*Schmackeria*)	*serricaudatus* (T. Scott)	Indian Ocean and west coast of Africa
,, ,,	*cornutus* Nicholls	South coast of Australia.

Brackish-water species.

P. (*Schmackeria*)	*annandalei* Sewell	Salt Lakes, Calcutta and Chilka Lake.
,, ,,	*tollingerae* Sewell	Salt Lakes, Calcutta and Chilka Lake.
,, ,,	*binghami* Sewell	Rangoon river estuary and Chilka Lake.
,, ,,	*daughlishi* Sewell	Kurau river, Perak.
,, ,,	*dubius* Kiefer	Vizagapatam Harbour.

Fresh-water species.

P. (*Schmackeria*)	*beieri* Brehm	Cambodia.
,, ,,	*brehmi* Kiefer	Philippine Islands.
,, ,,	*forbesi* Poppe & Richard	Yangtze-Kiang river.
,, ,,	*inopinus* Burckhardt	Yangtze-Kiang river.
	var. *gordioides* Brehm	Tongking.
,, ,,	*japonicus* Kikuchi (?=*inopinus* Burckhardt)	Japan.
,, ,,	*lobipes* Gurney	India.
,, ,,	*nostradamus* Brehm	East Java.
,, ,,	*pauliana* Brehm	Madagascar.
,, ,,	*poppei* Stingelin	Celebes.
,, ,,	*smithi* Wright	Philippine Islands.
,, ,,	*trihamatus* Wright	Celebes.

The distribution of the genus strongly suggests that the subgenus *Pseudodiaptomus* (s. str.) has spread from the western region of the Pacific through the Tethys Sea, the ancestral form of the American species reaching the Atlantic Ocean and becoming dispersed throughout the North and South Atlantic Gulfs, evolving into different species ; while a second form managed to get into the Indo-African Gulf and one daughter species, *hessei* Mrâzek, later managed to get carried round the Cape of Good Hope into the South Atlantic and became established in the Congo river estuary. The subgenus *Schmackeria* appears to have entered the Indo-Australian Gulf and in the brackish-water areas at the mouths of the rivers opening into the Bay of Bengal a number of species have been developed, one of which, *lobipes* Gurney, has penetrated into fresh water ; another species, *pauliana* Brehm, penetrated to the head of the Gulf and when the fissure between India and Antarctica opened up a passage into the Indo-African Gulf was able to reach Madagascar and also penetrated into fresh water. Finally one species, *cornutus* Nicholls, penetrated into the fissure between Australia and Antarctica and reached its habitat on the south coast of Australia. At some subsequent date the species, *serricaudatus* (T. Scott), was swept round the Cape of Good Hope and so reached the west coast of Africa, where like *hessei* Mrâzek, it managed to establish itself in the estuaries of the Congo and Niger rivers.

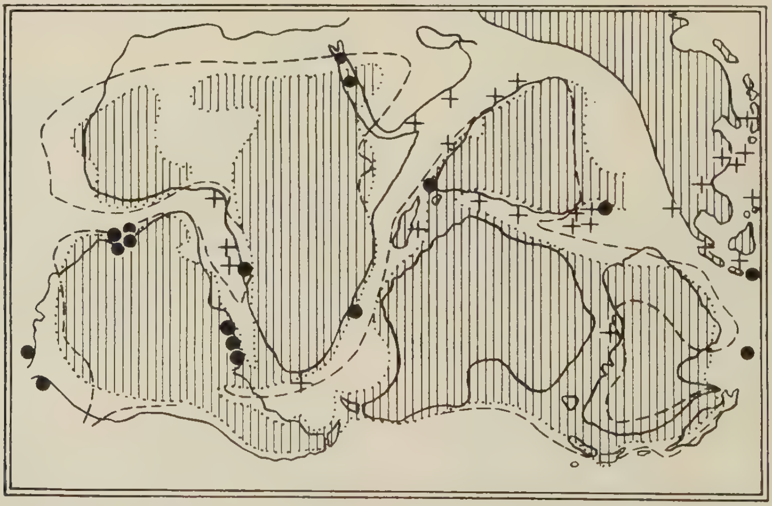

FIG. 12.—The same distribution of the two subgenera of the genus *Pseudodiaptomus* Herrick (s. lat.) plotted on the map of Gondwanaland in the late Cretaceous, according to du Toit.

The region at the head of the Bay of Bengal, which includes the estuaries of the Brahmaputra, Ganges and Mahanaddi rivers as well as the salt lakes of Calcutta and the Chilka Lake of Orissa, is an area that seems to be particularly favourable for the invasion by marine forms into brackish water and in Appendix II, I have given a list of the species that have been recorded from this region : many of these have been recorded from marine habitats in the western Pacific and may, like the species recorded from the Baltic Sea (*vide supra*, p. 166), have been swept in by the coastal currents ; others have been established for a sufficiently long time to have developed into varieties. Sars (1905) has reported on a collection of brackish-water species that was taken in Chatham Island in the south-west Pacific, some 300 miles to the east of New

Zealand : his list includes 11 species, five of which occur also in the Indian region, namely :

Ectinosoma melaniceps (Boeck) (=*australis* Brady) ;
Idyaea furcata (Baird) ;
Mesochra meridionalis Sars ;
Laophonte chathamensis Sars ; and
Halicyclops propinquus Sars.

Of these the first two are cosmopolitan species, so that their presence in the two areas is not surprising ; but of the last three, *Laophonte chathamensis* is only known in addition from the region of the Cape of Good Hope, and the other two have so far not been recorded from any other locality. Furthermore, there are in addition several other species in the Bay of Bengal area that are very closely related to Chatham Island species, namely :

Acartia southwelli Sewell closely related to *A. simplex* Sars ;
Cyclopina minuta Sewell closely related to *C. pusilla* Sars ;
Nitocra vahiai Blanchard & Richard closely related to *N. fragilis* Sars ; and
Laophonte bengalensis Sewell closely related to *L. chathamensis* Sars.

Thus out of the 11 Chatham Island species there are 9 in the Bay of Bengal area that are either identical or very closely related. This high degree of similarity between the faunas of the two areas, which are now separated from each other by some 5,400 miles, can hardly be accounted for on the supposition that such a group of species was swept passively by ocean and coastal currents from one region to another ; but if we plot the two areas on the map of Gondwanaland in the early Cretaceous, as proposed by du Toit (*vide* fig. 13) with Chatham Island close to New Zealand and this last much closer to Australia and accept du Toit's suggestion that certainly New Zealand and probably Chatham Island are parts of the Gondwanide anticline and only reached their present position in the late Cretaceous, it appears that the two regions were relatively close to the two ends of the fissure that separated Antarctica and Australia. When this fissure commenced to form probably the same process was carried out as in the case of the other lines of fracture ; a chain of lakes and rivers was first formed and as the gap between the two continents widened

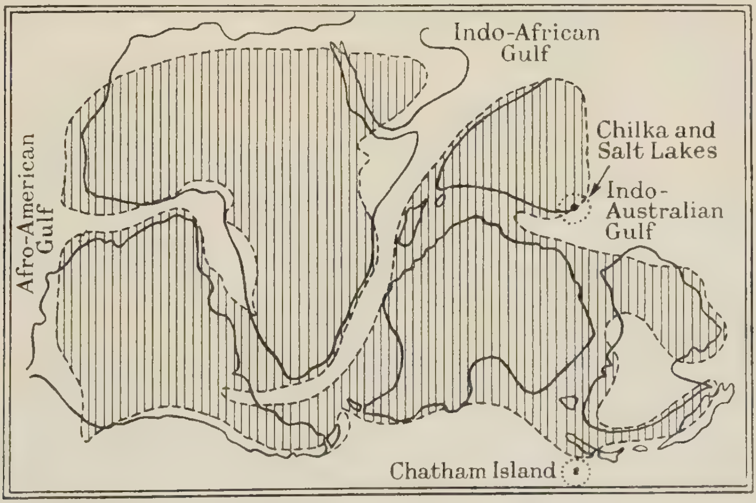

Fig. 13.—Map of Gondwanaland in the early Cretaceous (from du Toit) showing the positions of the Chilka and Salt Lake area and Chatham Island.

this crack became filled with water that was at first brackish, at any rate on the surface: if this were so, the spread of species from one area to another would have been comparatively easy. That such a migration of brackish-water forms might have taken place is also indicated by the present-day distribution of the genus *Gladioferens* Henry, to which I have already referred (*vide supra*), and the genus *Brunella* Smith,* in which species are now known from South-east Australia, Tasmania, South Australia and West Australia (*vide* fig. 8).

It thus appears that the present-day distribution, so far as we know it, of many of the Copepoda can better be accounted for on the supposition that (1) the group is a very old one and (2) the continents reached their present positions by a process of fracturing and drifting, as envisaged in the 'Continental Drift Theory', rather than by the older theory of the 'Permanence of the Ocean Basins'. It may be thought that I have laid too much stress on the view that a number of species may have existed practically unchanged since the Cretaceous: but I would point out that the evolution of marine organisms, owing to the stability of their habitat, is probably much slower than that of land animals, and I need hardly remind the zoological members of my audience of the great antiquity of such a species as *Lingula* in the Brachiopods and *Latimeria* in the Coelacanth fishes.

APPENDIX I.

A list of species of the Copepoda that have been recorded from brackish water in the three great oceans, Pacific, Indian and Atlantic.

PACIFIC OCEAN	INDIAN OCEAN	ATLANTIC OCEAN
Paracalanus crassirostris f. *typica*	*Paracalanus crassirostris* f. *sewelli*	*Paracalanus crassirostris* f. *scotti*
		Paracalanus parvus
	Paracalanus serratipes	
	Acrocalanus gibber	
Acrocalanus inermis	*Acrocalanus inermis*	
		Eucalanus attenuatus
		Eucalanus setiger
	Eucalanus subcrassus	
		Eucalanus vadicola
		Undinula vulgaris
		Nannocalanus minor
		Pseudocalanus elongatus
	Centropages alcocki	
		Centropages brachiatus
	Centropages furcatus	*Centropages furcatus*
		Centropages hamatus
	Centropages kroyeri	
Centropages mcmurrichi		
Gladioferens imparipes		
Gladioferens gracilis		
Gladioferens subsalaria		
Gladioferens spinosus		
		Pseudodiaptomus acutus
		Pseudodiaptomus americanus

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* Species of the genus *Brunella* Smith:

Brunella ampulla Searle	South-east Australia.
,, *attenuata* Fairbridge	West Australia.
,, *australis* Searle	South-east Australia.
,, *expansa* Sars	South-east Australia.
,, *longicornis* Searle	South-east Australia.
,, *salina* Nicholls	South Australia.
,, *steeli* Henry	New Zealand.
,, *subattenuata* Fairbridge	West Australia.
,, *tasmanica* Smith	Tasmania.
,, *viridis* Searle	South-east Australia.

Pacific Ocean	Indian Ocean	Atlantic Ocean
	Pseudodiaptomus annandalei	
Pseudodiaptomus aurivillii	*Pseudodiaptomus aurivillii*	
Pseudodiaptomus beieri		
	Pseudodiaptomus binghami	
Pseudodiaptomus brehmi		
		Pseudodiaptomus coronatus
		Pseudodiaptomus cristobalensis
Pseudodiaptomus culebrensis		
	Pseudodiaptomus dauglishi	
	Pseudodiaptomus dubius	
Pseudodiaptomus forbesi		
		Pseudodiaptomus gracilis
		Pseudodiaptomus hessei
	Pseudodiaptomus hickmani	
Pseudodiaptomus inopinus		
	Pseudodiaptomus lobipes	
		Pseudodiaptomus marshi
Pseudodiaptomus mertoni	*Pseudodiaptomus mertoni*	
Pseudodiaptomus nostradamus		
	Pseudodiaptomus pauliana	
		Pseudodiaptomus pelagicus
Pseudodiaptomus poppei		
		Pseudodiaptomus richardi
		Pseudodiaptomus serricaudatus
Pseudodiaptomus smithi		
	Pseudodiaptomus stuhlmanni	
	Pseudodiaptomus tollingerae	
Pseudodiaptomus trihamatus		
	Isias tropica	
		Temora longicornis
	Temora stylifera	*Temora stylifera*
	Temora turbinata	
		Lucicutia flavicornis
		Labidocera acuta
		Labidocera acutifrons
		Labidocera brunescens
Labidocera euchaeta	*Labidocera euchaeta*	
		Labidocera fluviatilis
	Labidocera gangetica	
	Labidocera kroyeri var. *bidens*	
Labidocera lubbocki		
	Labidocera pavo	
	Labidocera pectinata	
		Labidocera scotti
	Pontella andersoni	
		Pontella gaboonensis
	Pontella investigatoris	
	Tortanus barbatus	
	Tortanus forcipatus	
		Acartia bifilosa
	Acartia centrura	
	Acartia chilkaensis	
Acartia clausi	*Acartia clausi*	*Acartia clausi* var. **gaboonensis**
		Acartia denticornis
		Acartia discaudata
		Acartia forcipata
		Acartia giesbrechti
	Acartia plumosa	*Acartia plumosa*
Acartia pacifica	*Acartia pacifica*	
	Acartia southwelli	
	Acartia spinicauda	
		Acartia tonsa

Pacific Ocean	Indian Ocean	Atlantic Ocean
	Acartiella gravelyi	
	Acartiella major	
	Acartiella minor	
	Acartiella sewelli	
	Acartiella tortaniformis	
		Paracartia dubia
		Paracartia grani
Paracyclopina nana		
		Cyclopina gracilis
	Cyclopina intermedia	
	Cyclopina longifurca	
	Cyclopina minuta	
Cyclopina pusilla		
	Halicyclops aequorius	
Halicyclops propinquus	*Halicyclops propinquus*	
Halicyclops sinensis		
	Halicyclops tenuispina	
Halicyclops thermophilus		
	Dioithona indo-gallica	
		Oithona amazonica
		Oithona atlantica
Oithona brevicornis	*Oithona brevicornis*	
	Oithona horai	
		Oithona minuta
Oithona nana	*Oithona nana*	
		Oithona similis
Oithona simplex		
		Oncaea conifera
		Oncaea obtusa
		Oncaea venusta
		Corycaeus amazonicus
		Corycaeus speciosus (as *C. varius*)
	Corycaeus subtilis	
	Longipedia coronata	
	Longipedia rosea	
	Canuella furcigera	
		Ectinosoma curticorne
Ectinosoma melaniceps	*Ectinosoma melaniceps*	
	Ectinosoma normani	*Ectinosoma normani*
	Microsetella norvegica	
	Harpacticus gracilis	
	Harpacticus littoralis	
	Parategastes sphaericus var. *similis*	
	Idyaea furcata	
	Idyaea ensifera	
	Dactylopusia brevicornis	
	Amphiascus scotti	
Amphiascus pacificus		
Schizopera longicornis		
Nitocra fragilis		
	Nitocra spinipes, var. *orientalis*	
	Nitocra typica, var. *lacustris*	
	Nitocra yahiai	
	Stenhelia inopinata	
	Stenhelia longifurca	
Mesochra meridionalis	*Mesochra meridionalis*	
	Mesochra nana	
Laophonte chathamensis	*Laophonte chathamensis*	
	Laophonte bengalensis	
	Laophonte quinquespinosa	
	Cleta secunda	
		Cleta lamellifera
	Cletocamptus confluens	*Cletocamptus confluens*
Cletocamptus retrogressus	*Cletocamptus retrogressus*	

APPENDIX II.

A list of marine and brackish-water species that have been taken in the Salt Lakes, Calcutta, the Hoogli river and the Chilka Lake.

Paracalanus crassirostris Dahl.
,, ,, f. *sewelli* Früchtl.
Acrocalanus inermis Sewell.
Isias tropica Sewell.
Pseudodiaptomus (*Pseudodiaptomus*) *aurivillii* Cleve.
,, ,, *hickmani* Sewell.
,, (*Schmackeria*) *annandalei* Sewell.
,, ,, *binghami* Sewell.
,, ,, *serricaudatus* (T. Scott).
,, ,, *tollingerae* Sewell.
Labidocera gangetica Sewell.
,, *pavo* Giesbrecht.
Pontella andersoni Sewell.
Acartia (*Acartiura*) *chilkaensis* Sewell.
,, ,, *southwelli* Sewell.
,, (*Odontocartia*) *centrura* Giesbr.
,, ,, *spinicauda* Giesbr.
Acartiella major Sewell.
,, *minor* Sewell.
,, *tortaniformis* Sewell.
Oithona brevicornis Giesbr.
,, *horai* Sewell.
,, *nana* Giesbr.
Cyclopina intermedia Sewell.
,, *longifurca* Sewell.
,, *minuta* Sewell.
Halicyclops aequorius Fischer.
,, *propinquus* Sars.
,, *tenuispina* Sewell.
'*Saphirella indica*' Sewell.
Corycaeus (*Onychocorycaeus*) *giesbrechti* F. Dahl.
Longipedia coronata Claus.
,, *rosea* Sars.
Canuella furcigera Sars.
Harpacticus littoralis Sars.
,, *gracilis*, var. *orientalis* Sewell.
Paralegastes sphaericus (Claus), var. *similis* Sewell.
Idyaea furcata Baird.
,, *ensifera* Fischer, var. *indica* Sewell.
Ectinosoma melaniceps Boeck.
,, *normani* T. & A. Scott.
Microsetella norvegicas Boeck.
Dactylopusia brevicornis (Claus).
Amphiascus scotti Sewell (=*Dactylopus propinquus* T. Scott).
Stenhelia inopinata (A. Scott).
,, *longifurca* Sewell.
Mesochra meridionalis Sars.
,, *nana* Brady.
Nitocra spinipes Boeck, var. *orientalis* Sewell.
,, *typica* Boeck, var. *lacustris* Sewell.
,, *yahiai* (Blanchard & Richard).
Laophonte bengalensis Sewell.
,, *chathamensis* Sars.
,, *quinquespinosa* Sewell.
Cleta secunda Sewell.
Cletocamptus confluens (Schmeil).
Euterpina acutifrons (Dana).

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SYSTEMATICS ASSOCIATION.

ANNUAL REPORT XIV (1954–55).

The thirteenth Annual General Meeting was held in the rooms of the Geological Society, Burlington House, Piccadilly, on Wednesday, May 19, 1954.

The Species Concept in Palaeontology.

A colloquium with this title followed the Annual General Meeting on 19 May 1954. Contributions to the colloquium will be published. Mr. P. C. Sylvester-Bradley has kindly agreed to act as editor.

Presentation of Biological Distributions.

A pamphlet on the symposium held in conjunction with the Royal Geographical Society (1950) has at last been published and distributed to members.

International Botanical Congress, Paris, 1954.

The Association was represented by Prof. D. H. Valentine, Prof. T. G. Tutin, Dr. H. G. Baker and Dr. J. G. Hawkes at a discussion entitled " The Progress of Work on the European Flora ", mentioned in last year's report. The discussion showed that there was a wide diversity of opinion amongst European botanists as to what work should be done, and how it could be done. It was clear that there is, at present, little hope of international co-operation on the projected European Flora, though a less ambitious scheme, such as a check-list, may prove feasible.

Index of Botanical Research on European Plants.

An index of research undertaken by British botanists has been published through the International Association for Plant Taxonomy, and is enclosed with this report. It is hoped that a more complete index may be available later this year, or at the beginning of 1956, and that similar publications (possibly on a wider basis) may thenceforth appear annually.

The National Collections.

An interesting discussion on future policy in relation to the National Zoological and Botanical Collections was held in the rooms of the Linnean Society on 24 February 1955. Speakers included Dr. B. M. Hobby, Mr. J. E. Lousley, Mr. E. Milne-Redhead and Dr. W. B. Turrill. After careful consideration, the Council has decided that the contributions to the discussion are not, as a whole, suitable for publication.

Taxonomic Principles Committee.

The principles of the Deme Terminology have been outlined in a paper published by Mr. J. S. L. Gilmour and Prof. J. Heslop-Harrison in *Genetica XXVII* (1954), 147–161. Reprints of this paper have been circulated to members.

Retirement of Mr. P. C. Sylvester-Bradley.

After many years of valuable service to the Committee, Mr. P. C. Sylvester-Bradley has felt obliged to retire from the office of Convener. Mr. J. Lewis (Kew) has kindly agreed to take his place.

SYSTEMATICS

General Account

INCOME	£	s.	d.
Balance at Westminster Bank 4 May 1954	156	18	11
Annual Subscriptions	57	5	0
Donations		10	0
Clarendon Press : royalties on " The New Systematics "	14	13	6
Sales of " Bibliography of Key Works "	47	13	5
	£277	0	10

Special Account

	£	s.	d.
Balance in Post Office Savings Bank 4 May 1954	327	7	4
Life Memberships—2	10	0	0
Transfer from General Account *re* sales			
" Bibliography of Key Works " *re* 1953–54	23	7	5
do. do. *re* 1954–55	30	0	0
Interest 1954	8	7	8
	£399	2	5

Balance Sheet

LIABILITIES	£	s.	d.
Founder and Life Members—44	220	0	0
Annual subscriptions in advance—101	25	5	0
Creditor : Hon. Zoological Secretary (January–9 May 1955)	4	14	6
Excess assets over liabilities	582	19	6
	£832	19	0

Audited and found correct—
VICTOR S. SUMMERHAYES,
E. MILNE-REDHEAD.
16 May 1955.

ASSOCIATION

1954-55

EXPENDITURE	£	*s.*	*d.*
Hon. Zoological Secretary's expenses (January 1954–January 1955)	10	1	10
Hon. Botanical Secretary's expenses (May 1952–April 1955)		10	5
Hon. Treasurer's expenses (16 January 1954–10 April 1955)	2	17	1
Couldrey & Co. : duplicating paper	3	0	0
Meeting in rooms of Geological Society, with tea	2	15	0
do. Linnean Society	1	15	0
Reprints : R. Geographical Society	24	0	0
do. : Taxon	3	7	0
Transfers to Special Account *re* sales of Bibliography			
29 May 1954 *re* 1953–54	23	7	5
29 October 1954	30	0	0
Balance at Westminster Bank 6 May 1955	175	7	1
	£277	0	10

Due to Special Account *re* sales of Bibliography	£17	3	5

1954-55

	£	*s.*	*d.*
Balance in Post Office Savings Bank 6 May 1955	399	2	5
	£399	2	5

May 6th, 1955

ASSETS	£	*s.*	*d.*
Balance in Post Office Savings Bank	399	2	5
Balance at Westminster Bank	175	7	1
Subscribers one year in arrear, 46 @ 4*s*.	9	4	0
Subscribers two years in arrear, 22 @ 4*s*.	4	8	0
" Bibliography of Key Works . . . "			
Doubtful debts, 5 copies		7	6
Copies sold recently but not settled, 3 (@ 7*s*. 6*d*.)	1	2	6
Copies unsold 649 (valued @ 7*s*. 6*d*.)	243	7	6
	£832	19	0

G. J. KERRICH,
Honorary Treasurer,
11 May 1955.